FISHERY BOARD OF SWEDEN

INSTITUTE OF FRESHWATER RESEARCH

DROTTNINGHOLM

Report No 38

LUND 1957
CARL BLOMS BOKTRYCKERI A.-B.

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Avkastningen av gädd- och abborrfisket vid Sveriges östersjökust under åren 1914—1955

The yield of the pike and perch fisheries along the Baltic coasts of Sweden during the years 1914—1955

By Gunnar Alm

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I. Inledning

I den svenska östersjökustens bräckta vatten förekommer utom vissa saltvattensfiskar samt de anadroma arterna lax och ål även flertalet rena sötvattensfiskar. Särskilt för det egentliga skärgårdsfisket spelar vissa av de senare en mycket stor roll. Viktigast är gädda (*Esox lucius* L), abborre (*Perca fluviatilis* L) och sik (*Coregonus* sp.). Den senare fångas huvudsakligen i de nordligare länen, medan de båda andra förekommer tämligen allmänt utmed hela kuststräckan. I rätt stor utsträckning fångas även braxen (*Abramis brama* L), mört (*Leuciscus rutilus* L) och id (*Leuciscus idus* L).

Ofta framkommer från såväl yrkes- som sportfiskare klagomål över nedgång i utbytet av särskilt gädda och abborre. Det är då av intresse att närmare undersöka, om en sådan nedgång föreligger, eller om det endast är fråga om fluktuationer i utbytet eller i fiskbeståndet, och i så fall om några orsaker härtill kan påvisas. Av vikt är härvid att om möjligt undersöka, hur lekfisket utövas, och om någon inverkan härav kan påvisas i ena eller andra riktningen. Särskilt för ufärdandet av rationella fiskestadgar är kännedom om dessa förhållanden av värde.

II. Material

Alltsedan år 1914 föreligger för kustfisket en tämligen god fångststatistik, uppdelad på de olika länen. Här finnes alltså ett underlag för diskussion av berörda spörsmål. Ihågkommas bör då, att denna statistik endast omfattar yrkes- och husbehovsfisket. Fångsten vid sportfisket ingår däremot ej. I verkligheten ligger därför värdena för främst gädda, men även abborre, betydligt högre än vad siffrorna utvisar. Detta gäller särskilt de senaste åren, då sportfisket ökat i hög grad. Primärmaterialet för årsfångsterna återfinnes i Sveriges officiella statistik, Fiske, och är här ej medtaget. Förutom från denna statistik har en del tidigare fångstuppgifter hämtats ur vissa hushållningssällskaps årsredogörelser, delvis publicerade, delvis tillhörande Fiskeristyrelsens arkiv. Vidare har genom vänlig förmedling av professor HALME, Helsingfors, och fiskeriinstruktör WESTLING på Åland vissa uppgifter erhållits över Finlands kustfiske efter gädda och abborre.

För bedömandet av ovanberörda frågor är det viktigt att även veta, under vilka tider på året som de egentliga fångsterna görs. Genom välvilligt tillmötesgående från några av de större fiskförsäljningsföreningarna vid Sve-

Tabell 1. Fiskförsäljningsföreningar, varifrån erhållits uppgifter över månadstillförseln. — *Fish marketing associations which have supplied information about the monthly catches.*

Namn	Adress	För åren
Stockholms läns fiskförsäljningsförening	Stockholm	1949—1955
Södermanlands läns »	Nyköping	1945—1955
Östergötlands läns »	Norrköping	1948—1955
Västerviks »	Västervik	1952—1955
A/B Västerbofisk	Oskarshamn	1945—1955
S. Kalmar läns fiskförsäljningsförening	Kalmar	1949—1955
Blekinge läns »	Karlskrona	1946, 1952—1955

riges ostkust ävensom från vissa enskilda fiskgrossister har det varit möjligt att för ett större eller mindre antal år erhålla uppgifter över tillförseln av gädda och abborre under olika månader. Föreningarnas inköpsområden representerar de viktigare fångstlänen.Med hänsyn till att en stor del av fångsten vid kusten (25—100 %) numera går genom dessa föreningar, ger denna månadsfördelning en god bild av själva fångstens växlingar under året. Endast undantagsvis tillförs fisk från insjöarna. I tabell 1 har upptagits namnen på dessa uppgiftslämnare samt de år, för vilka uppgifter erhållits. För att ej utlämna de sålunda erhållna uppgifterna till offentligheten har för samtliga områden och år uträknats månadsfångsten i procent av årsfångsten. De härvid erhållna värdena har återgivits på ett stort antal diagram. Däremot har de primärtabeller, varpå figurerna baserats, ej införts i texten, enär detta ansetts onödigt tyngande.

Till samtliga personer, som på ett eller annat sätt lämnat mig ovannämnda värdefulla material, uttalar jag här mitt varma tack.

III. Medelavkastningen för 5-årsperioder av de viktigaste sötvattensfiskarna vid Sveriges östersjökust

I figur 1 återgives medelårsfångsten för 5-årsperioder för de viktigare vid svenska östersjökusten fångade sötvattensfiskarna. Härav framgår att utbytet av samtliga arter uppvisar stora förändringar under de olika perioderna. Fångstkurvan för sik stiger kraftigt under senare perioder, vilket i viss mån även gäller braxen. Fångstkurvan för mört sjunker däremot i stort under hela 40-årsperioden. Vad angår gädda och abborre, som frånsett de senaste åren givit det största utbytet, visar kurvorna en viss höjning, dock med svag nedgång för de båda senaste 5-årsperioderna. Påfallande är därjämte en viss överensstämmelse i fångstutbytets förändringar hos dessa båda arter. Det är också endast de som nu närmare skall behandlas.

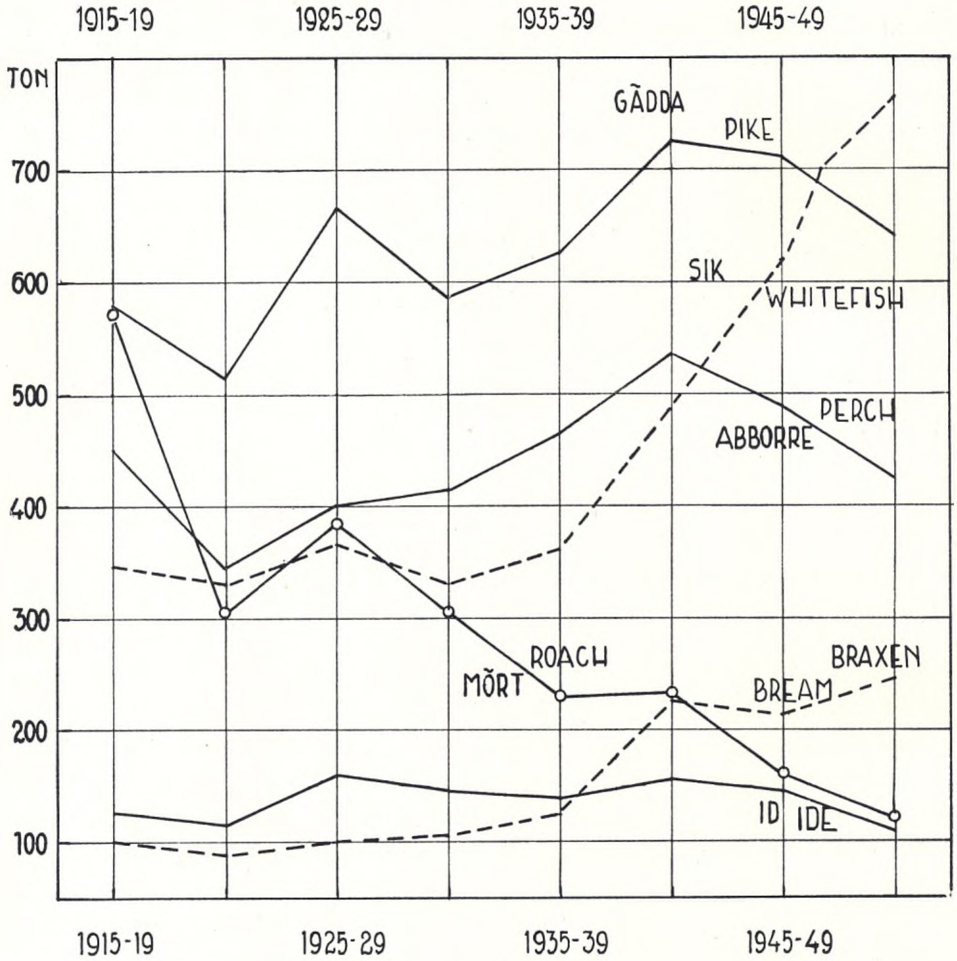

Fig. 1.

Avkastningen i ton av de viktigare vid Sveriges östersjökust fångade sötvattensfiskarna. Årsmedeltal för 5-årsperioder.

Yield in tons of the more important fresh-water fish caught along the Baltic coast of Sweden. Yearly average in 5-years periods.

IV. Kort översikt av gäddans och abborrens biologi, fångst och förekomst vid Sveriges kuster

Både gädda och abborre är typiska skärgårdsfiskar. Merendels är de ganska stationära och gör oftast blott mindre vandringar mellan de grundare lekområdena och de djupare vattnen såväl i innerskärgårdarna som i yttre havsbandet (EKMAN TH. 1915, GOTTBERG 1923, HESSLE 1934). En del av gäddbeståndet företar under sommaren regelbundna sådana vandringar till ytterskärgårdarna (SEGERSTRÅLE, C. 1948). Större exemplar av båda arterna övergår ibland till ett mera rörligt levnadssätt och följer då särskilt strömming- och norsstimmen. Strömming, (*Clupea harengus* L), nors (*Osmerus eperlanus* L), löja (*Alburnus lucidus* L), mört (*Leuciscus rutilus* L), kvidd (*Phoxinus aphya* L), spigg (*Gasterosteus* sp.) och tånglake (*Zoarces viviparus* L), utgör huvudfödan för gäddan och den större abborren. Den mindre abborren håller sig till diverse smådjur, framförallt insektlarver, *Asellus-*, *Mysis-* och *Gammarus*-arter samt plankton. Också skorv, *Idotea,* uppges av SEGERSTRÅLE utgöra en viktig föda för abborren.

Leken förrättas hos båda arterna ibland i innerskärgårdarna på relativt grunt vatten i gräsbeväxta vikar, i övrigt på en halv till två m djup över mattor av »rödgräs» (*Chara* sp.) och andra vattenväxter samt över tångflader (*Fucus*), och beträffande abborren över stengrund och ris. Gäddan leker även på de lösslitna tångansamlingar, som är vanliga i skärgårdarna. Särskilt gäddan går ofta upp mot mynningarna av utfallande smärre vattendrag för att förrätta sin lek. I de södra länen leker gäddan vanligen i april —maj, i de mellersta och nordligare länen från slutet av april till in i början av juni, undantagsvis ända framåt midsommar. (EKMAN, TH. 1907, SEGERSTRÅLE, C. 1947, 1948). Av viss betydelse är också strändernas nord- eller sydläge. Särskilt i innerskärgårdarna och i lugnare vikar blir, liksom fallet är i sjöarna, vattnet på våren tidigare uppvärmt utmed de solbestrålade nordstränderna än vid de mindre solexponerade sydstränderna (WESENBERG-LUND 1912, ALM 1926). Detta medför att leken sker tidigare i förra än i senare fallet. Den individuella lektiden varar några veckor, men redan viss tid före leken infinner sig åtminstone hanarna på lekplatsen. Vidare sker leken tidigare i de inre än i de yttre skärgårdarna. Abborren leker i allmänhet något senare än gäddan, och t.o.m. den 1 juli träffas ibland abborre som ännu ej lekt (SEGERSTRÅLE, C. 1948). Det nykläckta gäddynglet sitter som bekant 10—15 dagar mest fastsuget vid vattenväxter. Därefter håller det sig tämligen stilla i skydd av vegetationen. Abborrynglet lever omedelbart efter kläckningen fritt i mera öppet vatten, men sluter sig snart samman i stim som håller till bland vegetation nära stränderna.

Tillväxten är redan från början betydligt hastigare hos gäddan än hos abborren. Enligt föreliggande undersökningar över ålder och tillväxt hos gädda och abborre vid Östersjöns kuster (GOTTBERG 1917, NILSSON 1921, ROSÉN 1920, SEGERSTRÅLE, C. 1948) kan som allmän regel sägas att gäddan vid 3, 4 och 5 års ålder har en längd av resp. 30—40, 35—45 och 45—55 cm. Fångståldern omfattar 3—7 år, vanligast 4—5 år. Abborren uppnår vid en ålder av 5, 6, 7 och 8 års ålder vanligen en längd av 15—20, 19—22, 21—25 och 22—30 cm. Vanligaste fångståldern torde vara 5—10 år. Hos båda arterna växer honorna fr.o.m. andra eller tredje året bättre än hanarna (GOTTBERG 1917, SEGERSTRÅLE 1948, ALM 1952) varför större exemplar vanligen är honor.

Fångsten av både gädda och abborre, s.k. fjällfisk, sker framförallt med

Tabell 2. Fångsten i ton och i % av hela kustfångsten av gädda och abborre i de viktigare länen. Medeltal för åren 1915—1955. — *Catches of pike and perch in the more important provinces, expressed in tons and as percentages of the total yield of the coastal fisheries. Average for the years 1915—1955.*

	Gädda		Abborre	
	Ton	%	Ton	%
Norrbottens län	24,3	3,9	34,1	7,7
Stockholms län	102,6	16,3	77,8	17,7
Södermanlands län	44,—	7,—	46,8	10,6
Östergötlands län	80,9	12,9	51,—	11,6
Kalmar län	196,8	31,3	142,0	32,3
Gotlands län	29,—	4,6	—	—
Blekinge län	91,7	14,6	18,8	4,3
Övriga län	59,7	9,4	69,5	15,8
Hela kusten *The whole coast*	629		440	

ryssjor, i synnerhet för gäddan under leken. Härvid begagnas såväl vanliga små ängsryssjor som storryssjor av olika format och längre söderut även bottengarn. De båda senare kommer särskilt till användning i de yttre skärgårdarna på de djupare lekplatserna, men även längre in för fångst av gädda på väg till de grundare lekvikarna samt vid de mera öppna men tämligen långgrunda havsstränderna inom stora delar av södra Kalmar län. I de större ryssjetyperna görs ofta mycket givande abborrfångster. Både gädda och abborre tas vidare i stor utsträckning på nät av olika slag. På en del håll har under senare år nylonnät vunnit stort insteg och används nu även under vårfisket. Noten är också ett flitigt använt redskap i skärgårdarna. Och härtill kommer slutligen olika slags krokredskap.

Fisket utövas såväl av den jordbruksidkande befolkningen som även av rena yrkesfiskare. De senare ägnar vissa årstider åt detta fjällfiske, medan de i övrigt bedriver fiske efter torsk, flundra, lax och framförallt strömming. Härtill kommer då det ovannämnda sportfisket som utövas av fritidsfiskare.

Gäddans och abborrens natur av skärgårdsfiskar gör dem givetvis beroende av förekomsten av sådana biotoper som är typiska för skärgårdarna. Utmed stora delar av norrlandskusten är skärgårdsutvecklingen utom längst i norr, rätt svag, varför trots kustens längd gädda och abborre icke i större omfattning finner för dem lämpliga biotoper. Annat är förhållandet vid kusterna av Stockholms, Södermanlands och Östergötlands län, vid norra delen av Kalmar län och i Blekinge län, där stora skärgårdar och långa kuststräckor förenas och erbjuder goda betingelser för rika bestånd av både gädda och abborre. Omkring Öland, delvis även Gotland samt utmed södra Kalmar läns mera öppna kuster förekommer mångenstädes grundare strandplatåer med rik tång och annan vattenvegetation, där båda arterna finner goda biotoper.

Avkastningen av gädd- och abborrfisket vid den svenska östersjökusten är därför ganska olika i de olika länen. Tabell 2 visar medelårsfångsten för

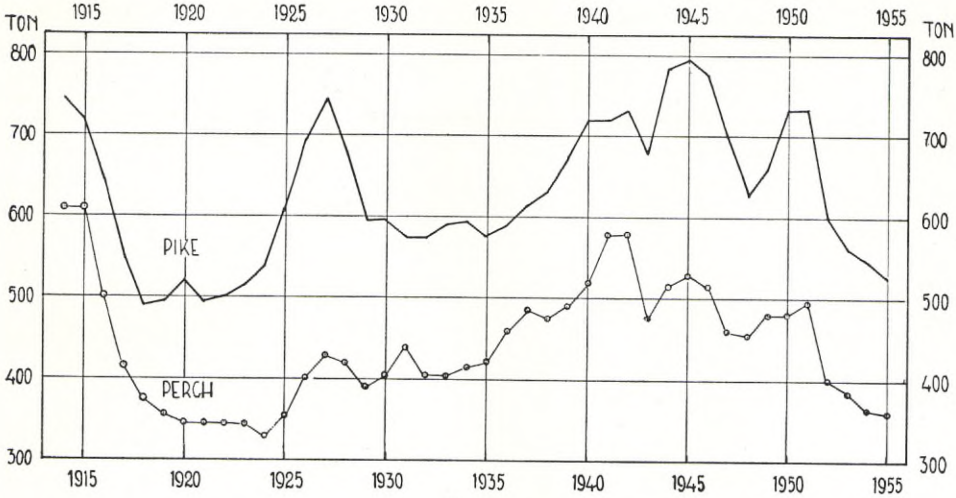

Fig. 2.

Årsfångsten i ton av gädda och abborre vid Sveriges östersjökust.

Annual catch in tons of pike and perch along the Baltic coast of Sweden.

hela perioden, fördelad på de viktigare länen. Härav synes att fångsten av såväl gädda som abborre är störst i Kalmar län. Därnäst kommer Stockholms, Östergötlands och Blekinge län. Vid Gotland fås tämligen mycket gädda, medan abborren är mera sparsam. Vid övre Norrland-kusten är förhållandet det motsatta. För hela kusten har under statistikperioden fångsten av gädda och abborre uppgått till i genomsnitt 629 resp. 440 ton per år. Gäddfångsten ligger alltså med omkring 40 % över abborrfångsten.

I detta sammanhang bör även framhållas att dessa fiskarter är mycket vanliga även vid Finlands östersjökust, som också erbjuder goda biotoper för dem båda. Enligt C. SEGERSTRÅLE (1948) uppgick år 1934 fångsten av gädda till 998 ton och av abborre till 1.307 ton. Och år 1953 fångades enligt LIEDES (1955), 1.773 resp. 1.724 ton gädda och abborre. Största gäddfångsten kom år 1934 på Åbo-Björneborgs län och på Åland med resp. 485 och 255 ton. År 1953 togs däremot endast 164 ton gädda på Åland men över 800 ton vid kusterna av sydvästra och södra Finland. Abborren tas huvudsakligen i Åboskärgården, men även i stor mängd i Finska viken. Vid Österbottenkusten är som på svenska sidan abborren ofta viktigare än gäddan.

V. Avkastningen av gädd- och abborrfisket under olika år

Fig. 2 utvisar årsfångsten av gädda och abborre vid svenska östersjökusten under hela perioden. Härav framgår dels att fångstmängden varierar mycket under olika år och perioder, dels att den förut nämnda överensstämmelsen i dessa fluktuationer hos de båda arterna är långt större än som synes

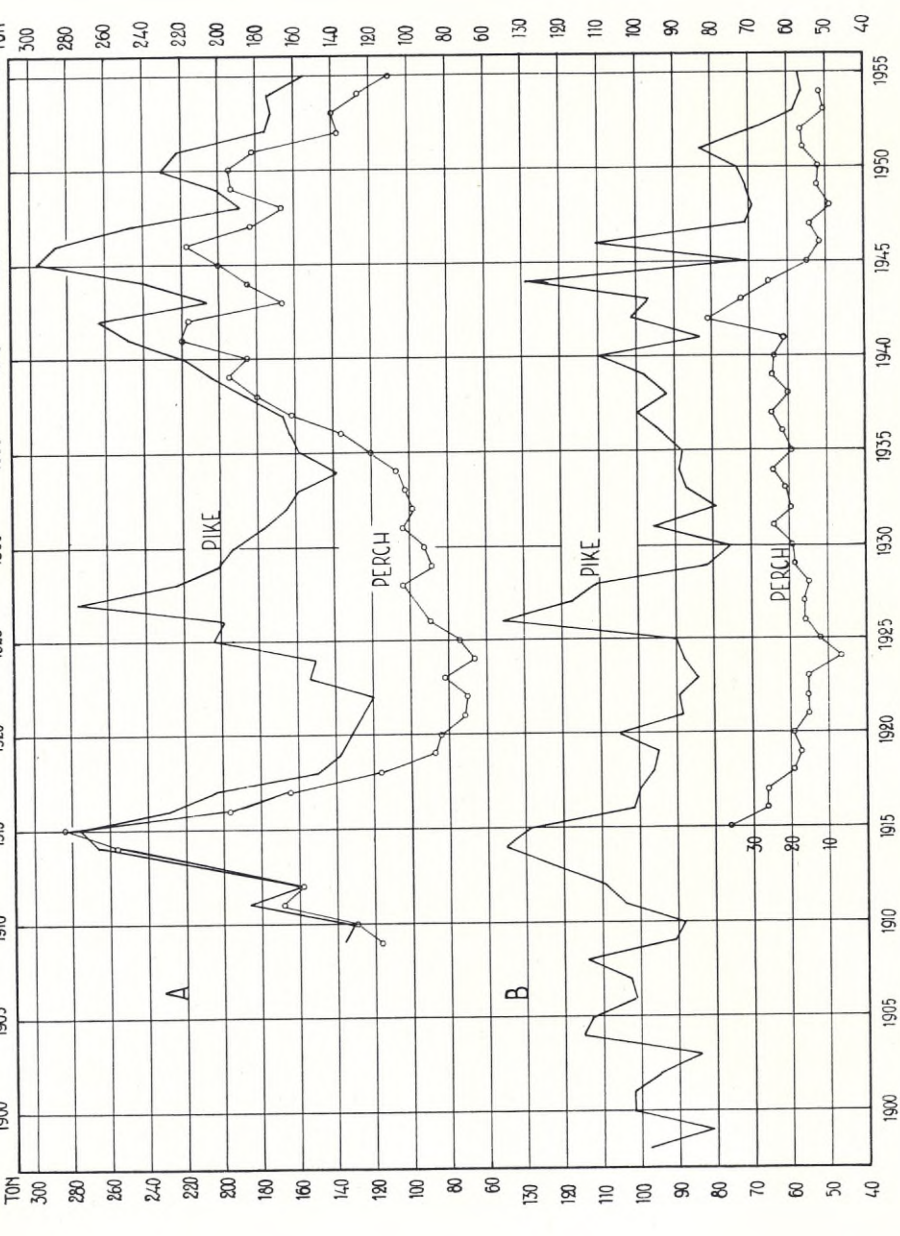

Fig. 3.

Årsfångsten i ton av gädda och abborre vid kusten av (A) Kalmar och (B) Blekinge län.

Annual catch in tons of pike and perch along the coasts of the provinces of Kalmar (A) and Blekinge (B).

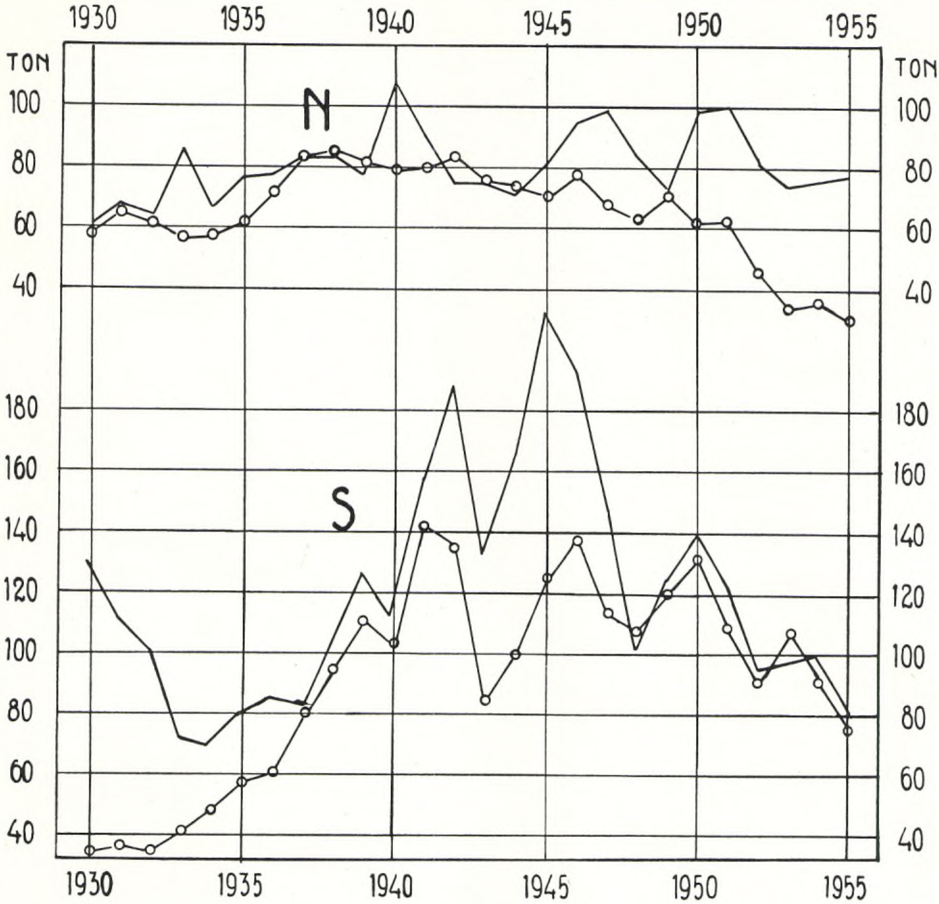

Fig. 4.

Årsfångsten i ton av gädda och abborre vid kusten av (N) norra och (S) södra Kalmar län.
Annual catch in tons of pike and perch along the coasts of the northern (A) and southern (B) part of the province of Kalmar.

av 5-årsvärdena. Särskilt påfallande är fångsttopparnas likhet under åren 1914—15, 1941—42, 1944—46 och 1950—51. Den stora toppen i gäddkurvan åren 1926—28 motsvaras också av en viss uppgång i abborrkurvan.

Förhållandena är emellertid olika i olika län, och fångstkurvorna för hela kusten blir i viss mån beroende av fångsten i det län, där det största utbytet erhålles, nämligen Kalmar län. Som framgår av fig. 3 återfinnes här ännu mera utpräglat än för hela kustkurvorna de fem nyssnämnda topparna. Överhuvudtaget frapperas man, frånsett det stora utbytet, av de synnerligen stora både lång- och kortvariga fluktuationerna i detta län. Iögonfallande är därjämte överensstämmelsen i upp- och nedgång i fångsten av båda arterna, särskilt under de senare 20 åren. I figur 4 har för åren fr.o.m. 1930 en upp-

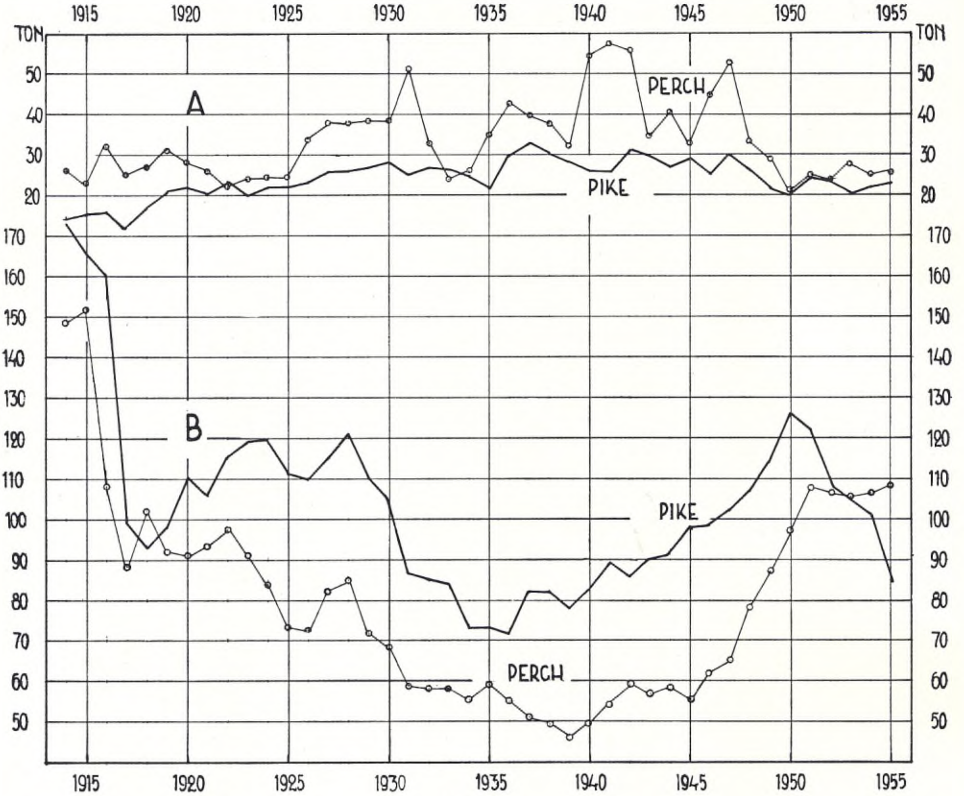

Fig. 5.

Årsfångsten i ton av gädda och abborre vid kusten av (A) Norrbottens och (B) Stockholms län.

Annual catch in tons of pike and perch along the coasts of the provinces of Norrbotten (A) and Stockholm (B).

delning skett på norra och södra delarna av Kalmar län. Gränsen går då mellan Västervik och Oskarshamn. Öland tillhör sålunda södra delen. Man finner, att det framförallt är i denna del av länet som de stora fluktuationerna förekommer. Vidare är fångsten av både gädda och abborre merendels större här. Och slutligen är likheten i fluktuationerna för de båda arterna långt mera påfallande än i länets norra del, där endast mindre, mera oregelbundna fluktuationer förekommer. Det är således södra länsdelens avkastningskurvor, som på grund av de stora fångstmängderna, och än mera fluktuationernas storlek, i hög grad sätter sin prägel på kurvorna för hela kusten.

På figur 3 har även inlagts fångstkurvor för Blekinge län. För gäddan finner man större årsfångster under i vart fall några av de för Kalmar län utmärkande goda åren omkring 1915, 1926 och 1944—46. Det i södra Kalmar län givande året 1945 motsvaras däremot i det angränsande Blekinge län av

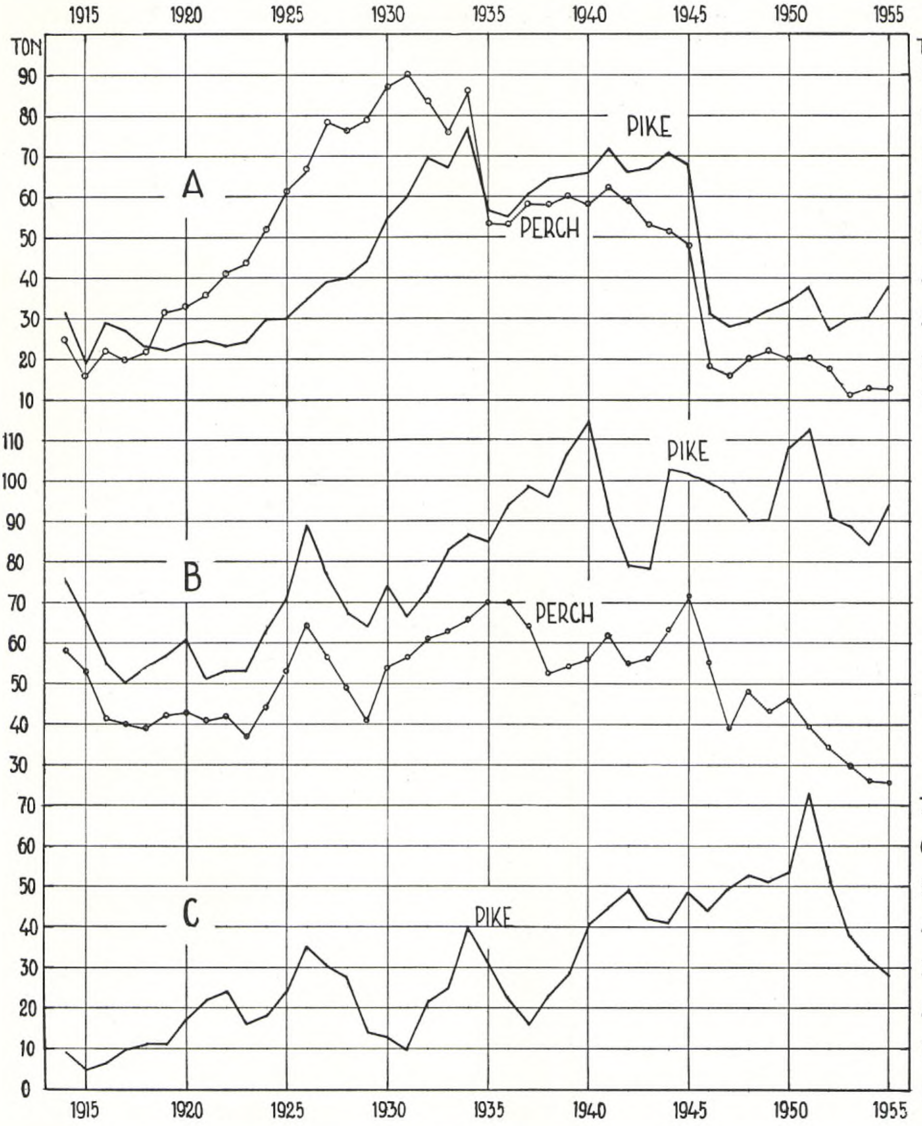

Fig. 6.

Årsfångsten i ton av gädda och abborre vid kusten av (A) Södermanlands, (B) Östergötlands och (C) Gotlands län.

Annual catch in tons of pike and perch along the coasts of the provinces of Södermanland (A), Östergötland (B) and Gotland (C).

mycket dålig fångst. Viss, ehuru mycket svag överensstämmelse mellan gäddfångsten och abborrfångsten synes föreligga.

I figur 5 återges fångstkurvor för Stockholms län samt för jämförelse även för Norrbottens län. I senare fallet framträder inga större förändringar, endast mera kortvariga fluktuationer, särskilt påfallande för abborrfångsten. Någon likhet i kurvornas förlopp förefinnes ej. För Stockholms län föreligger däremot en påtaglig sådan likhet, om man ser på kurvornas förlopp i stort. En jämförelse med figur 3 visar även att viss överensstämmelse råder med hela kustkurvorna. Det höga utbytet år 1915, viss nedgång omkring 1920 och uppgång åren 1924—28 för gädda, delvis också för abborre, återfinnes sålunda både för länet och för hela kusten. Därefter följer emellertid i länet en nedgångsperiod, som för båda arterna varar längre än för kusten i sin helhet. Slutligen kommer under 1940-talet en tämligen jämnt ökande uppgångsperiod, varefter följer lägre fångstsiffror för gädda under de senaste åren. Också uppgången på 1940-talet har viss motsvarighet i kustkurvorna.

För Södermanlands och Östergötlands län (fig. 6) visar gädd- och aborrkurvorna sinsemellan en ganska god överensstämmelse. Södermanlands län avviker från kustkurvan genom mycket låga fångster under periodens början samt en kraftig nedgång i mitten av 1940-talet. Detta sista har emellertid konstaterats bero på viss oförklarlig ändring i statistikinsamlingen. Siffrorna för de senare åren torde emellertid vara riktiga. Frånsett denna ovisshet rörande siffrorna för 1930- och första 1940-talen är här att observera att fångsten av abborre under åren fram till mitten av 1930-talet överstiger fångsten av gädda, medan förhållandet därefter är omvänt. Beträffande Östergötlands län uppvisar kurvorna likhet med dem för hela kusten. Toppar i fångsten för gädda kommer sålunda även här på åren 1914, 1926, 1940, 1945 och 1951. Aborrkurvan uppvisar tidigare större likhet med gäddkurvan än under senare år. Medan gäddkurvan i stort visar en ökande avkastning, håller sig abborrkurvan mera likformig under hela perioden, dock med nedgång under de senaste 10 åren. I Gotlands län slutligen visar gäddkurvan — abborren är här på grund av sin fåtalighet ej medtagen — rätt stora fluktuationer. Påfallande är den stadigt ökande fångsten. Och trots lägre fångster de fyra senaste åren, ligger dock dessa värden betydligt högre än under de tidigaste åren.

Denna översikt visar att fluktuationerna i fångsten av gädda och abborre ej förlöper helt lika i samtliga län. Tydligt är dock att, framförallt ifråga om gäddan men i viss grad även för abborren, vissa år eller perioder givit goda fångster i flertalet fall, medan andra varit dåliga över stora delar av kusten. Som sådana goda fångstperioder kan anföras åren omkring 1915, 1926, 1941, 1945—46 och 1950—51. Allmänt dåliga var åren i början av 1920- och 1930-talen samt åren 1952—54.

Det hade givetvis varit intressant att i detta sammanhang göra en jämförelse med eventuella fluktuationer i fångsten av dessa fiskarter i Finland och framförallt på Åland. Tyvärr är dock uppgifter härom mycket tunnsådda. HAGMAN (1946) har emellertid framlagt siffror för gäddfångsten för åren 1890—1919 vid Kökar och Brändö, båda i Ålands skärgård. Dessutom har från fiskerikonsulenten WESTLING på Åland erhållits fångstuppgifter för gädda och abborre för åren 1949—55. I förra fallet visar fångsten vid Kökar mycket stora fluktuationer med toppar åren 1896—97, 1901, 1908, 1912—14 och 1918—19. HAGMAN framhåller därjämte att även vid Brändö fångsten visat uppgång under i stort sett samma år som vid Kökar. Fångstsiffrorna för perioden 1949—1955 är med undantag för 1949 mera jämna, varierande mellan för gäddan 185 och 207 ton, och för abborren 50 och 75 ton. År 1949 gav 74 ton abborre, medan gäddfångsten uppgick till 278 ton. Enligt uppgift låg fångsten på liknande höga värden även åren närmast före, utan att dock siffror häröver föreligger (jmf sid. 39). Någon likhet mellan fluktuationerna i gädd- och abborrfångsten på Åland och på den svenska östersjökusten, närmast då Stockholms län, föreligger ej. Här ökar ju fångsten kraftigt under senare 1940-talet och sjunker åter först under 1952 och följande år.

VI. Gädd- och abborrfångsten under olika månader

I figurerna 7—9 har grafiskt återgivits fångsternas fördelning per månad i procent av årstillförseln inom de i tabell 1 upptagna områdena. Figur 7 återger densamma såsom medelvärden för samtliga år för både gädda och abborre. Figurerna 8 och 9 utvisar fördelningen för varje år och varje art för sig. I tabellerna 3 och 4 har ett sammandrag gjorts av procentsiffrorna för tre fångstperioder. Den första, *a,* omfattar månaderna före leken, d.v.s. januari—mars. Den andra, *b,* omfattar själva lekmånaderna. Härvid har för gäddan endast räknats med april och maj, trots att leken längre norrut fortgår in i juni. För hela östersjökusten torde dock de två månaderna i stort täcka den egentliga lekperioden. För abborren däremot pågår normalt leken såväl under längre tid som senare än hos gäddan. Det har därför synts riktigt att räkna med tre månader för abborrens lektid. Den tredje, *c*-perioden täcker årets samtliga återstående månader.

Vad först angår gäddan synes av figur 7 att i samtliga län huvudfångsten sker i endera av eller i båda månaderna april och maj. Detta bekräftar det i och för sig välkända faktum, att en stor del av fångsten sker under eller i samband med lektiden. Ibland, främst i Nyköping-området kommer en höjning också på hösten. Vidare synes att inom vissa områden, t.ex. Kalmarområdet, fångsten är mycket koncentrerad till lektiden, medan den t.ex. i Stockholm-området är mera fördelad på hela våren. Vid de tre områdena i Kalmar län märkes en mindre nedgång under förvåren. Detta kommer också fram inom Norrköping-området. Orsaken härtill torde mest vara att det under vintern givande krokfisket efter gädda (mest sax) försvåras och någon tid upphör när islossningen kommer. Vid den tiden har lekfisket ännu

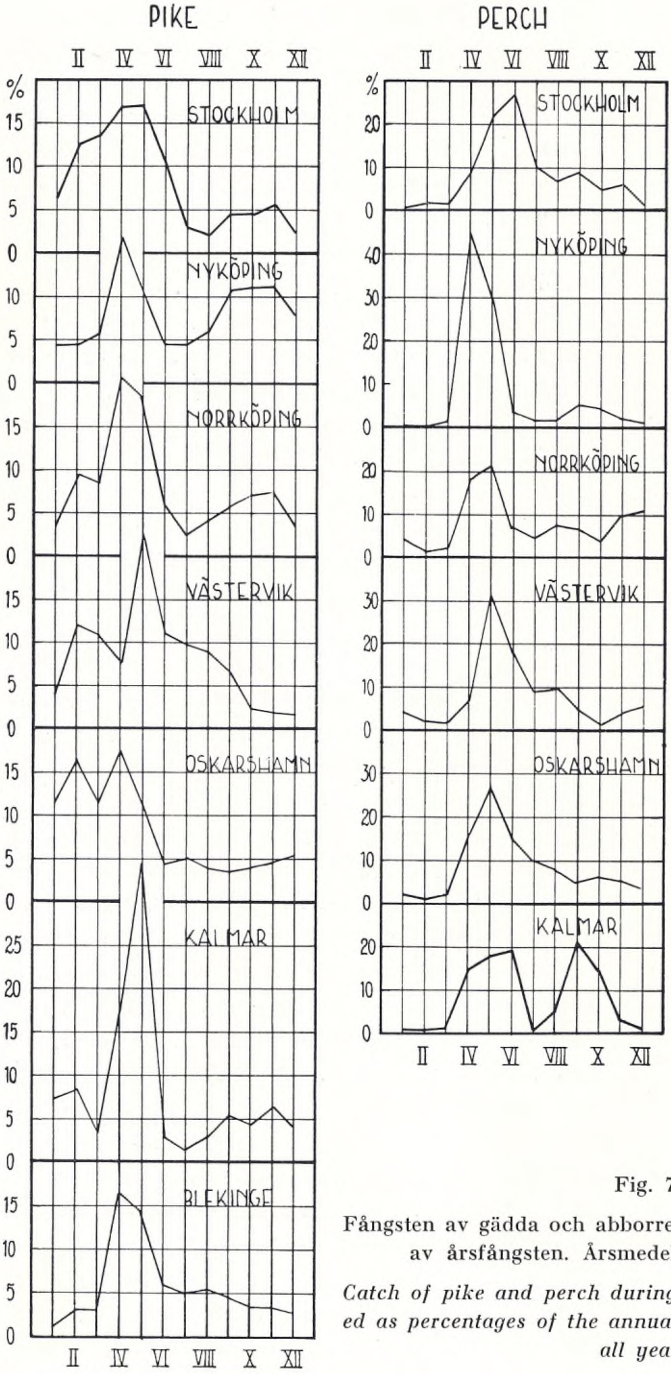

Fig. 7.

Fångsten av gädda och abborre under olika månader i % av årsfångsten. Årsmedeltal för samtliga år.

Catch of pike and perch during different months expressed as percentages of the annual catch. Yearly average for all years.

inte börjat i större omfattning. Stundom uppgives också att man på grund av lågt pris frivilligt begränsar kustgäddfisket vid den tid, då den största mängden gädda kommer i handeln från insjöarna, där leken sker tidigare än vid kusten.

Figur 8 visar att fångstfördelningen per månad varierar avsevärt under olika år, även om varje område har en för detsamma typisk fångsttid. Vissa år sker sålunda lekfångsten huvudsakligen under en enda månad, andra år är den utsträckt på flera månader. Ibland kommer största lekmånadsfångsten tidigt, ibland åter är den betydligt senare. Ofta är sådana förskjutningar gemensamma för flera län, så t.ex. den sena gäddlekfångsten år 1955. Södermanlands län visar hög höstfångstprocent under åren 1949, 1950 och 1955 och vidare några år en minskning under vårvintern, delvis sammanfallande med motsvarande nedgång i Stockholms län. Inom Östergötlands län är de olika årens fångstkurvor ganska lika. Under år 1952 saknas dock den annars karaktäristiska nedgången i mars. Denna nedgång kommer för Västervik vanligen i april, medan den för Oskarshamn och Kalmar faller på mars. I senare fallet saknas den helt de två senaste åren. För Oskarshamn märkes år 1949 en stark uppgång under hösten. Från Blekinge finnes i hushållningssällskapens årsberättelser ungefärliga uppgifter över månadsfångsten av gädda för åren 1900—1912. En genomgång av detta material har visat att även då stora variationer förekom i fångstens månadsfördelning. I genomsnitt för dessa år utgjorde fångsten under de tre perioderna resp. 23, 27 och 50 %. En påtaglig minskning av särskilt fångsten under a-perioden har sålunda inträtt under senare år, medan lekfångsten ökat något.

För abborren visar vårmånaderna april—maj men också juni den största fångsten. Detta motsvarar som ovan nämnts abborrens lektid, som ju delvis sammanfaller med gäddans, ehuru med större utsträckning och viss försening. Största relativa lekfångsten har Nyköping-området. För Kalmar-området märkes en kraftig uppgång i abborrfångsten även på hösten, sammanhängande med ett då givande revfiske. Beträffande de olika årens månadsfördelning gäller samma som för gäddan ifråga om särskilt lekfångstens varierande koncentration till en eller flera månader. Tydligt är emellertid att, trots dessa variationer, månadsfördelningen för de olika områdena behåller sin egenart. Särskilt tydligt framträder detta för Kalmar-området, där de två kraftiga fångsttopparna på vår och höst återkommer varje år.

De årliga växlingarna i fångstfördelningen medför givetvis vissa förskjutningar icke blott i lekfångstens procentuella storlek utan även i fångstprocenten för a- och c-perioderna. Av tabellerna 3 och 4 framgår att inom samtliga tre perioder finnas stora variationer. Tabellerna jämförda med figurerna visar emellertid att för samtliga områden i genomsnitt något över $^1/_3$ av årsfångsten av gädda och betydligt över $^1/_2$ av årsfångsten av abborre tas under lekperioderna. Under tiden före leken tas även en ganska stor mängd gädda, medan fångsten av abborre då är av mindre betydelse. Under årets senare

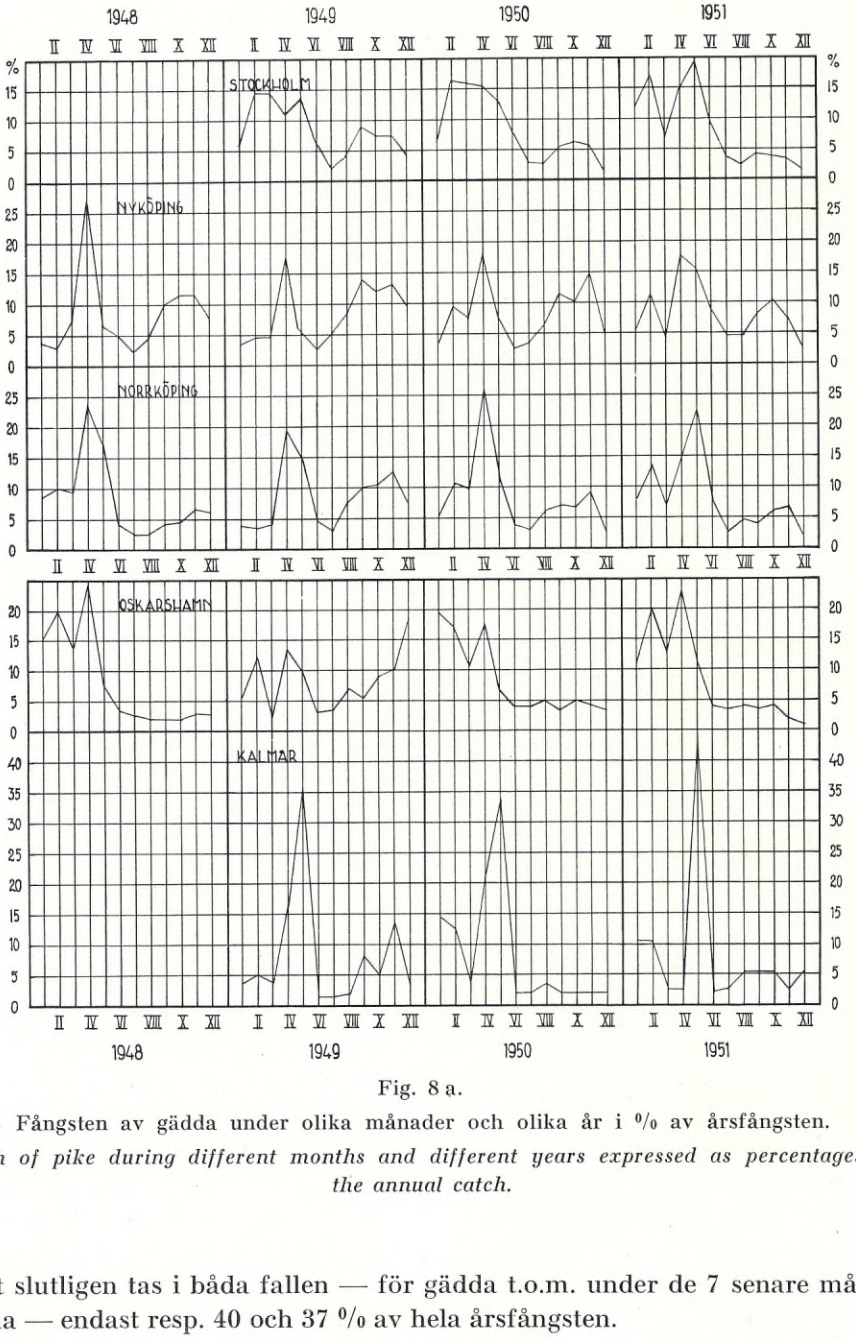

Fig. 8 a.

Fångsten av gädda under olika månader och olika år i % av årsfångsten.
Catch of pike during different months and different years expressed as percentages of the annual catch.

hälft slutligen tas i båda fallen — för gädda t.o.m. under de 7 senare månaderna — endast resp. 40 och 37 % av hela årsfångsten.

Ovan har antytts, att vissa likheter föreligger mellan de olika områdena beträffande fångstens månadsfördelning för olika år och särskilt för storleken av fångstprocenten under lektiden. Dessa procenttal utsäger dock ingenting om själva fångstens storlek. En hög lekfångstprocent förknippar

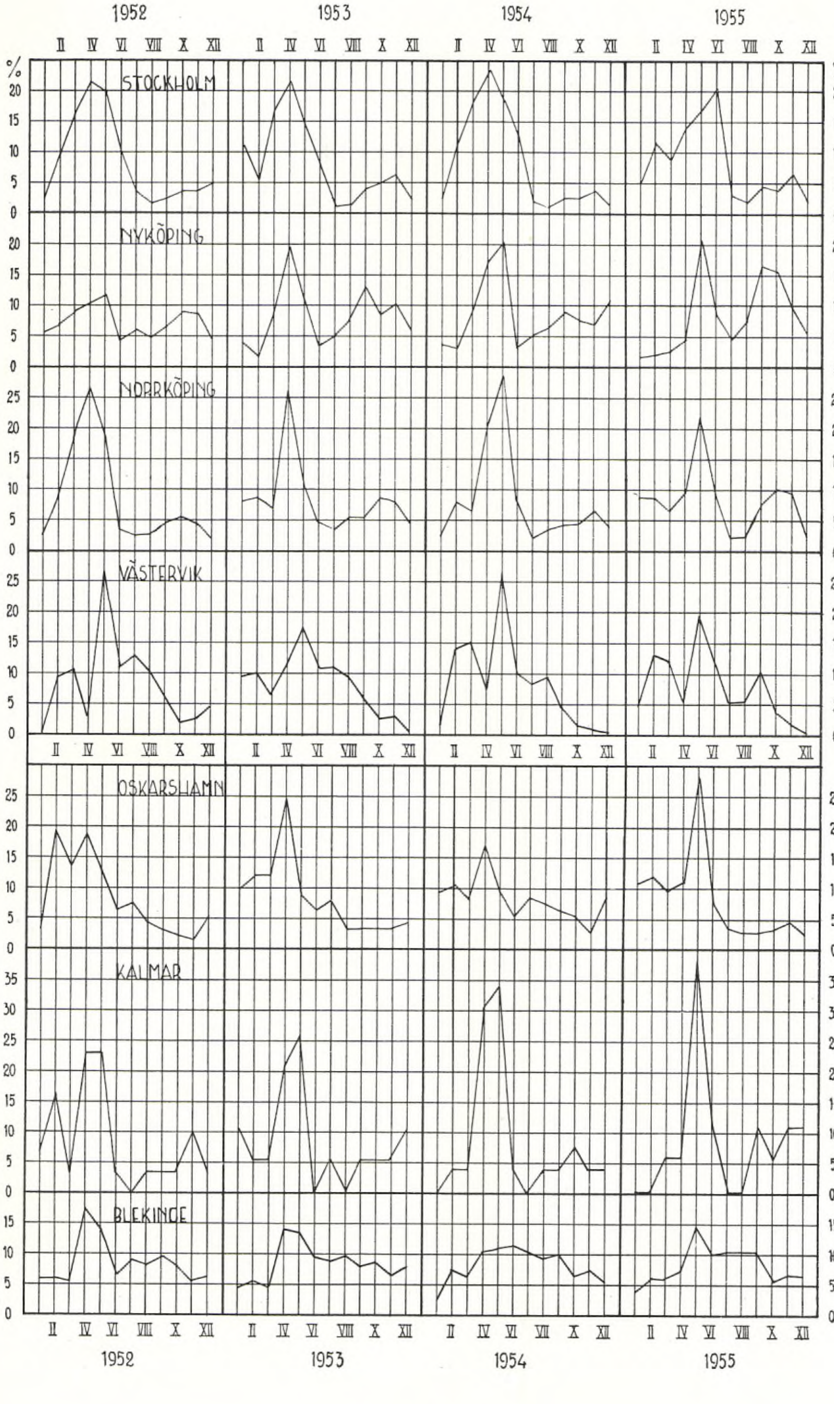
1952
1953
1954
1955
II IV VI VIII X XII
%
STOCKHOLM
NYKÖPING
NORRKÖPING
VÄSTERVIK
OSKARSHAMN
KALMAR
BLEKINGE
0
5
10
15
20
25
30
35

Fig. 8 b.

Fig. 9 a.

Fångsten av abborre under olika månader och olika år i $^0/_0$ av årsfångsten.
Catch of perch during different months and different years expressed as percentages of the annual catch.

man måhända gärna med en stor årsfångst. Teoretiskt bör emellertid en för ett visst år särskilt hög lekfångstprocent kunna förekomma både under goda och dåliga fångstår och tvärtom. Det är därför av intresse att jämföra fångstmängderna under året och under vardera av de tre perioderna med varandra. Då som inledningsvis nämnts föreningarnas tillförseluppgifter ej skall offentliggöras, har i stället en annan väg valts. Medelvärdena för såväl årsfångsten som för fångsten under vardera av a-, b- och c-perioderna har ta-


1952
1953
1954
1955
II IV VI VIII X XII
%
STOCKHOLM
NYKÖPING
NORRKÖPING
VÄSTERVIK
OSKARSHAMN
KALMAR
0
10
20
30
40
50
60

Fig. 9 b.

Tabell 3. Tillförseln av gädda under perioderna a (januari—mars), b (april —maj) och c (juni—december) i % av årstillförseln. Medeltal för samtliga år samt högsta och lägsta % tal. — *Supply of pike during the periods a (January—March), b (April—May), and c (June—December) expressed as percentages of the annual supply. Average for all years and highest and lowest percentage.*

Område	a			b			c		
	mt	max	min	mt	max	min	mt	max	min
Stockholm	33	39	25	34	42	25	33	43	25
Nyköping	15	21	13	29	38	20	56	68	44
Norrköping	24	30	11	39	45	31	37	55	26
Västervik	27	35	20	30	34	24	43	50	36
Oskarshamn	40	50	19	29	39	15	31	57	17
Kalmar	20	30	6	52	65	44	28	50	15
Karlskrona	15	17	13	32	57	21	53	62	30
Medeltal för samtliga områden *Average for all regions*	25			35			40		

gits som utgångspunkt, och de olika årens fångster har därefter uträknats i % av dessa medelvärden. I tabeller och figurer kommer de då att framstå som avvikelser från medelvärdena. Härvid har endast medtagits de områden, varifrån uppgifter föreligger för mera än fem år, och där fångsten utgjort en relativt stor del av länsfångsten. Detta gäller Stockholm-, Nyköping-, Norrköping- och Oskarshamn-områdena. De sålunda erhållna siffrorna har införts i tabellerna 5 och 6. I tabellerna har även som jämförelse införts de förutnämnda procenttalen för fångsten i b-perioden i förhållande till samma års totalfångst.

Början göres med gäddan under hänvisning till figur 10. I denna har in-

Tabell 4. Tillförseln av abborre under perioderna a (januari—mars), b (april — juni) och c (juli—december) i % av årstillförseln. Medeltal för samtliga år samt högsta och lägsta % tal. — *Supply of perch during the periods a (January—March), b (April—June), and c (July—December) expressed as percentages of the annual supply. Average for all years and highest and lowest percentage.*

Område	a			b			c		
	mt	max	min	mt	max	min	mt	max	min
Stockholm	4	11	2	57	74	43	39	48	24
Nyköping	2	7	1	78	90	65	20	29	9
Norrköping	8	20	3	46	68	28	46	64	29
Västervik	8	15	1	56	76	47	36	52	22
Oskarshamn	4	7	1	58	79	34	38	54	25
Kalmar	1	2	1	54	64	41	45	58	35
Medeltal för samtliga områden *Average for all regions*	5			58			37		

Tabell 5. Årstillförseln av gädda och tillförseln under olika perioder, allt uttryckt i %/o av medeltillförseln under samma tid. — *The annual supply of pike and the supply during different periods, all expressed in percentages of the average supply during the same time.*

Område	År	Tillförsel under				Lekfångst i % av årsfångst *Supply of spawning fish in per cent of the annual supply*
		Året	a	b	c	
Stockholm	1951	120	132	123	106	34
	1955	117	91	109	152	31
	1950	113	133	95	111	28
	1952	105	91	128	97	41
	1949	92	97	67	113	25
	1954	79	79	90	60	42
	1953	75	77	80	67	36
Nyköping	1955	136	60	121	162	25
	1950	117	163	102	112	25
	1951	117	169	136	93	33
	1954	117	126	151	98	38
	1953	99	97	106	95	30
	1946	95	87	81	102	25
	1945	81	71	57	94	20
	1949	93	74	78	105	24
	1952	86	123	105	66	35
	1947	86	57	79	96	27
	1948	81	77	94	74	33
Norrköping	1951	126	154	122	119	38
	1950	115	122	109	117	37
	1954	108	79	135	99	49
	1955	108	108	87	131	31
	1952	89	110	102	61	45
	1953	89	88	83	96	37
	1948	88	104	95	71	42
	1949	77	35	66	114	34
Oskarshamn	1950	142	164	116	124	25
	1951	135	145	153	93	34
	1945	130	151	105	115	24
	1946	109	133	55	117	15
	1952	105	96	111	100	32
	1947	97	71	118	100	37
	1948	88	106	100	46	34
	1955	87	71	113	71	39
	1949	87	41	68	151	24
	1954	75	53	66	102	27
	1953	71	61	79	71	33

förts fångstkurvor för dels de län, vari föreningarna är belägna, dels de relativa fångsterna inom dessas tillförselområden. Härav framgår att fångstkurvorna för länet och för området ifråga visar mycket stor överensstämmelse. Man kan därför utgå från att också den nedan berörda fördelningen under a-, b- och c-perioderna av föreningarnas årsfångster är typisk för gäddfångsten utmed här berörda kuststräckor och överhuvudtaget för östersjöfisket efter gädda.

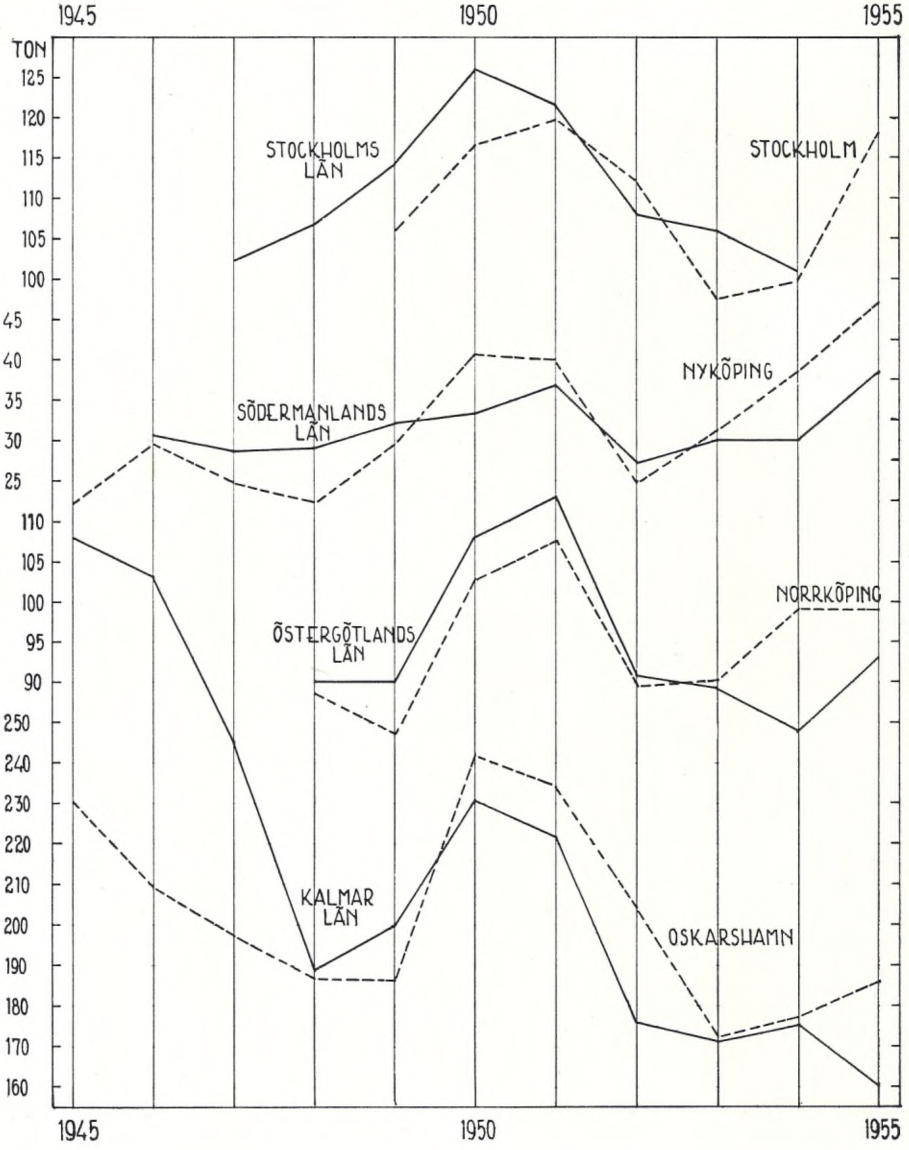

Fig. 10.

Gädda. Årsfångsten i ton i de viktigare länen (———) samt tillförseln till där befintliga föreningar i % av medeltillförseln (- - - - -).

Pike. Annual catch in tons in the more important provinces (———) and supply to their Fish marketing associations (- - - - -) expressed as percentages of the average supply.

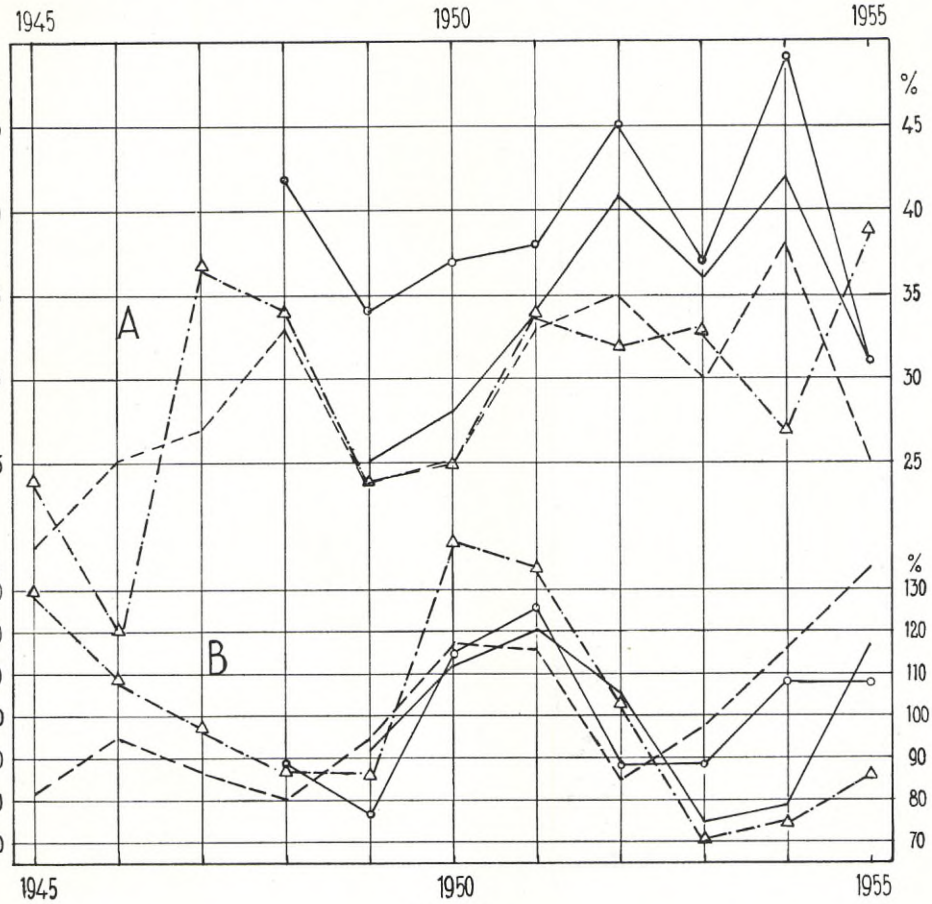

Fig. 11.

Gädda. A. Lekfångsten i $^0/_0$ av årsfångsten. B. Tillförseln i $^0/_0$ av medeltillförseln.
Pike. A. Catch of spawning fish in per cent of the annual catch. B. Supply in per cent of the average supply.
(——— Stockholm; — — — Nyköping; o———o Norrköping; △—·—·—△ Oskarshamn.)

På samma sätt som länsfångsterna sinsemellan visar stora likheter i upp- och nedgång kommer på grund av nu berörda överensstämmelse också fångstkurvorna för de fyra områdena att förlöpa likartat. Däremot föreligger, som figur 11 visar, föga överensstämmelse mellan variationerna i årsfångstens storlek och i procenttalen för lekfångsten. De senare visar dock sinsemellan i många fall ett likartat förlopp. Sålunda har desamma för Stockholm-, Nyköping- och Norrköping-områdena genomgående varit låga under åren 1949—50, 1953 och 1955 samt höga åren 1948, 1952 och 1954. Fångsten inom Oskarshamn-området uppvisar däremot en tämligen låg lekfångstprocent år 1954, men en hög sådan år 1955. Den höga lekfångstprocenten åren 1948 och 1954 motsvaras av rätt låga årsfångster samma år, medan under åren 1950 och 1955 med låg lekfångstprocent årsfångsten var hög. Åren 1949 och 1953 uppvisar å andra sidan både låg lekfångstprocent och låga årsfångster. Under år 1952 med hög lekfångstprocent var årsfångsten snarare låg än hög, och det goda fångståret 1951 hade för två områden en tämligen hög, men för två andra en relativt låg lekfångstprocent.

Då dessa frågor är av visst allmänt intresse har i figur 12 återgivits de i tabell 5 upptagna siffrorna för de tre fångstperioderna. Härvid bör ihågkommas att fångsten under a-perioden städse är mindre än under de övriga perioderna. Figuren visar flera intressanta förhållanden. De för samtliga fyra områden goda fångståren 1950 och 1951 har höga fångster under alla tre perioderna, men särskilt under a- och b-perioderna. Lekfångsten blir därför procentuellt medelmåttig. År 1955 med goda årsfångster i Stockholm-, Nyköping- och Norrköping-områdena utmärkes speciellt av höga fångster under c-perioden. Härigenom blir fångsten under lekperioden procentuellt rätt låg. Beträffande det för Nyköping- och Norrköping-områdena tämligen goda fångståret 1954 är det däremot lekfångstperioderna som givit goda fångster. Lekfångstprocenten är därför här mycket hög. Detta är också fallet i Stockholm-området, som emellertid samma år har låg årsfångst, Oskarshamn-området, också med låg årsfångst under år 1954, har däremot mycket dåliga fångster under a- och b-perioderna, medan c-perioden givit en ganska god sådan. Som följd härav blir lekfångstprocenten i motsats till för Stockholm-området låg. Det för samtliga områden dåliga fångståret 1949 har relativt höga fångster under c-perioden, men mycket låga fångster under både a- och b-perioderna. Här blir således lekfångstprocenten låg. År 1953, också tämligen dåligt överallt, har ganska låga fångster under alla tre perioderna. Lekfångstprocenten blir därför här högre än under år 1949, även om den alltjämt är tämligen låg.

Man finner sålunda att under de genomgående goda fångståren vanligen samtliga tre eller åtminstone två fiskeperioder, och därvid så gott som alltid b-perioden, givit höga fångster, medan under de dåliga fångståren antingen alla tre eller vanligen två perioder givit sämre utbyte. Vidare framgår att såväl hög som låg lekfångstprocent förekommit under både goda och dåliga fångstår.

Om någon större regelbundenhet ej kan utläsas ur dessa fakta, är emellertid påfallande, hur lika de olika fångstperiodernas värden år för år varit för olika områden. Tydligen har därför betingelserna för en bättre eller sämre fångst under dessa år varit desamma inom hela den berörda kuststräckan.

För abborren hänvisas till tabell 6 och figurerna 13—15. Vad först angår fångsten inom resp. län och inom de fyra föreningsområdena råder här ingen större överensstämmelse. Utom för Stockholm-området föreligger dock i båda fallen en tendens till lägre fångster under senare år. För samtliga föreningsområden utmärkande är dock liksom hos gäddan den höga års-

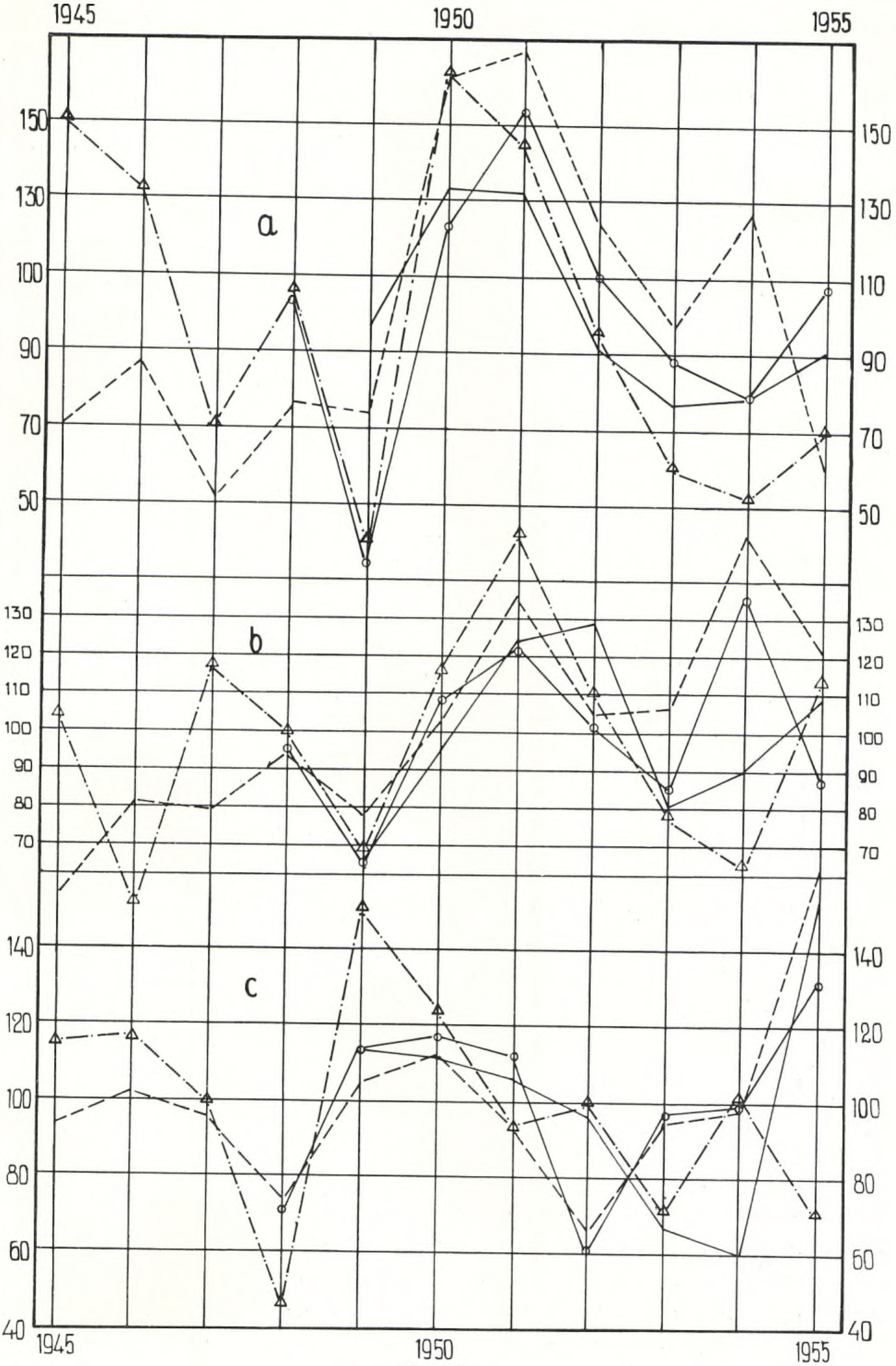

Fig. 12.

Gädda. Fångsten under a-, b- och c-perioderna (se texten) i % av medeltillförseln under dessa perioder.

Pike. Catch during the periods a-, b- and c (see the text) expressed as percentages of the average supply during these periods.

(——— Stockholm; — — — Nyköping; o———o Norrköping; △—·—·—△ Oskarshamn.)

Tabell 6. Årstillförseln av abborre och tillförseln under olika perioder, allt uttryckt i ⁰/₀ av medeltillförseln under samma tid. — *Perch. Cfr. Table 5.*

Område	År	Tillförsel under				Lekfångst i % av årsfångst *Supply of spawning fish in per cent of the annual supply*
		Året	a	b	c	
Stockholm	1955	127	70	93	156	50
	1949	124	330	113	148	43
	1951	119	70	117	126	57
	1950	100	70	115	82	66
	1952	91	30	95	93	58
	1954	71	30	93	44	74
	1953	64	30	78	44	70
Nyköping	1951	171	67	194	91	88
	1950	144	130	138	170	75
	1949	113	130	110	156	70
	1954	102	33	118	48	90
	1945	87	233	72	126	65
	1946	87	133	82	109	72
	1947	87	100	88	78	80
	1955	87	33	84	109	76
	1948	86	67	86	91	78
	1952	83	33	93	53	87
	1953	54	33	44	87	69
Norrköping	1950	134	90	138	138	47
	1949	119	289	85	123	33
	1955	103	33	90	127	40
	1948	101	100	62	140	28
	1951	96	100	115	75	55
	1952	97	133	108	79	51
	1953	81	67	90	73	51
	1954	72	33	106	44	68
Oskarshamn	1951	129	200	141	100	64
	1950	128	233	118	128	54
	1945	116	200	107	117	54
	1952	113	100	123	97	64
	1948	103	100	123	69	71
	1949	103	67	77	141	44
	1947	96	33	82	121	50
	1955	93	33	125	48	79
	1946	79	100	45	124	34
	1954	79	33	70	93	52
	1953	64	67	70	52	66

fångsten under något av eller båda åren 1950 och 1951 samt låg årsfångst under år 1953. Detta framträder tydligare på fig. 14 som visar årsfångstens och lekfångstprocentens växlingar. Den senare har för Stockholm-, Nyköping- och Norrköping-områdena liknande variationer för åren 1953—55, medan kurvan för Oskarshamn-området har ett helt motsatt förlopp.

Vad angår fångsten under de tre perioderna bör först ihågkommas att för abborren fångsten under a-perioden är helt obetydlig, endast omkring 5 ⁰/₀ av årsfångsten. Fig. 15 visar att under denna period mycket stora variationer

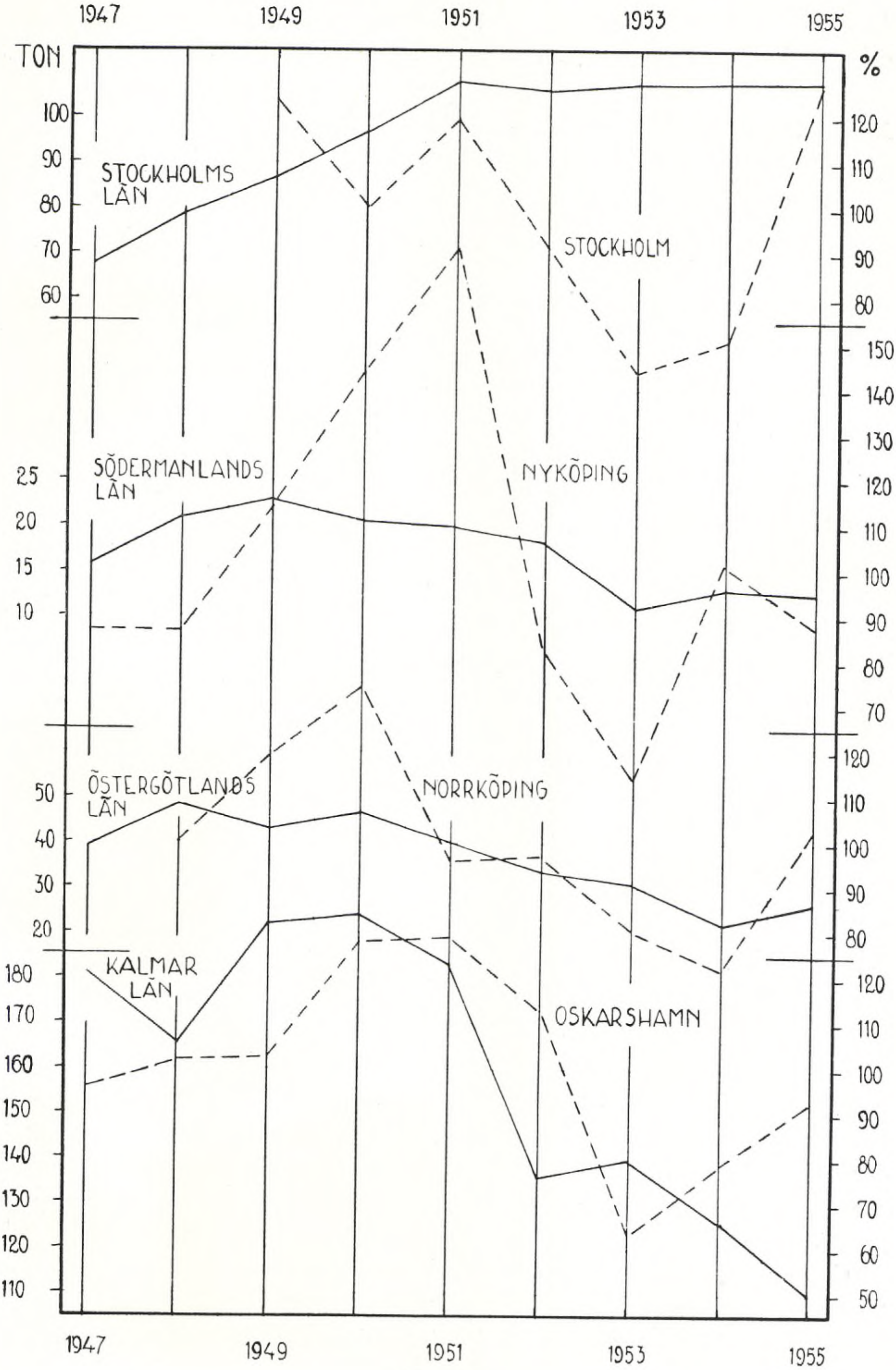

Fig. 13.

Abborre. Årsfångsten i ton i de viktigare länen (———) samt tillförseln till där befintliga föreningar i % av medeltillförseln. (- - - - -).

Perch. Annual catch in tons in the more important provinces (———) and supply to their Fish marketing associations (- - - - -), expressed as percentages of the average supply.

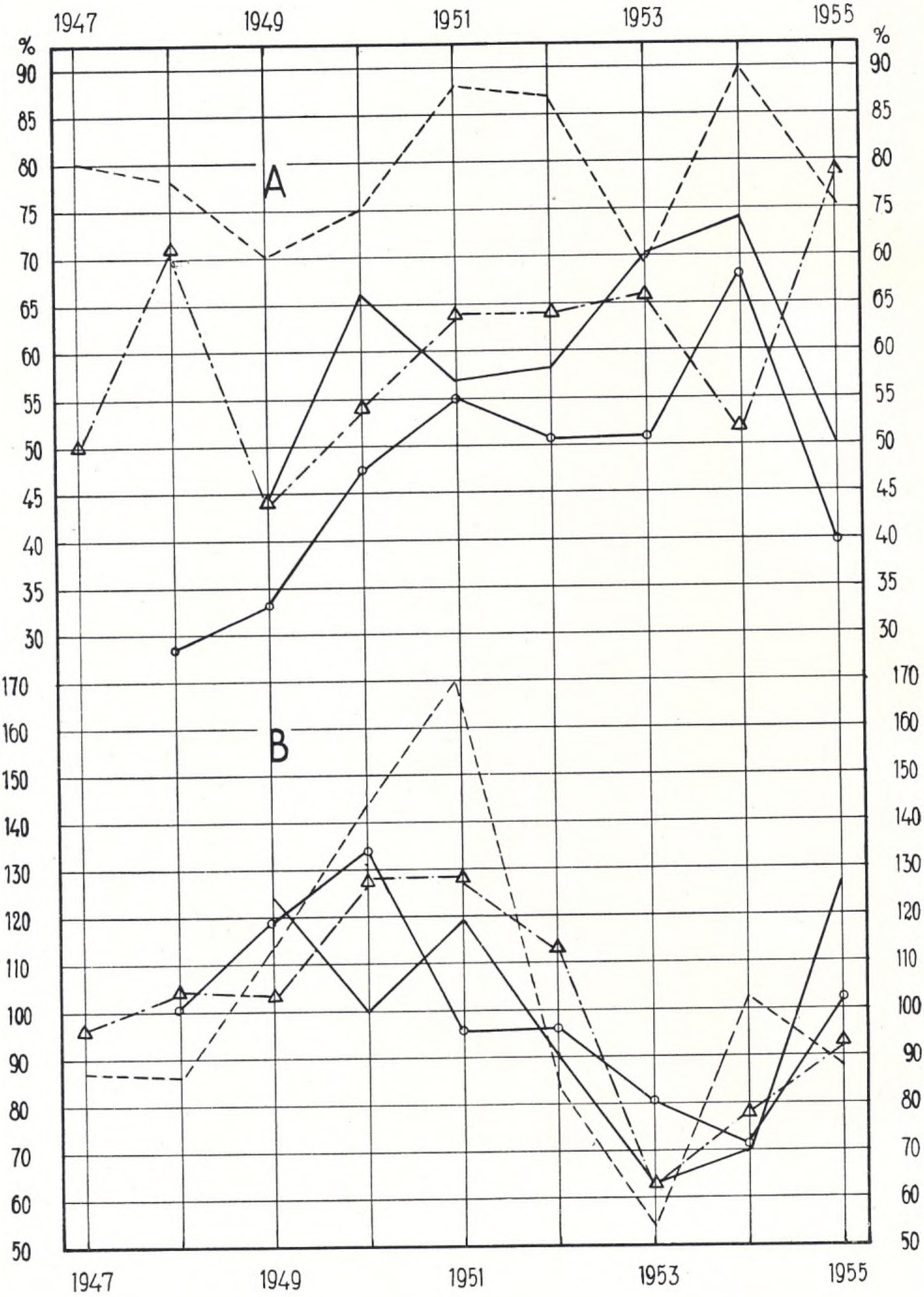

Fig. 14.

Abborre. A. Lekfångsten i $^0/_0$ av årsfångsten. B. Tillförseln i $^0/_0$ av medeltillförseln.

Perch. A. Catch of spawning fish in per cent of the annual catch. B. Supply in per cent of the average supply.

(——— Stockholm; — — — Nyköping; o———o Norrköping; △—·—·—△ Oskarshamn.)

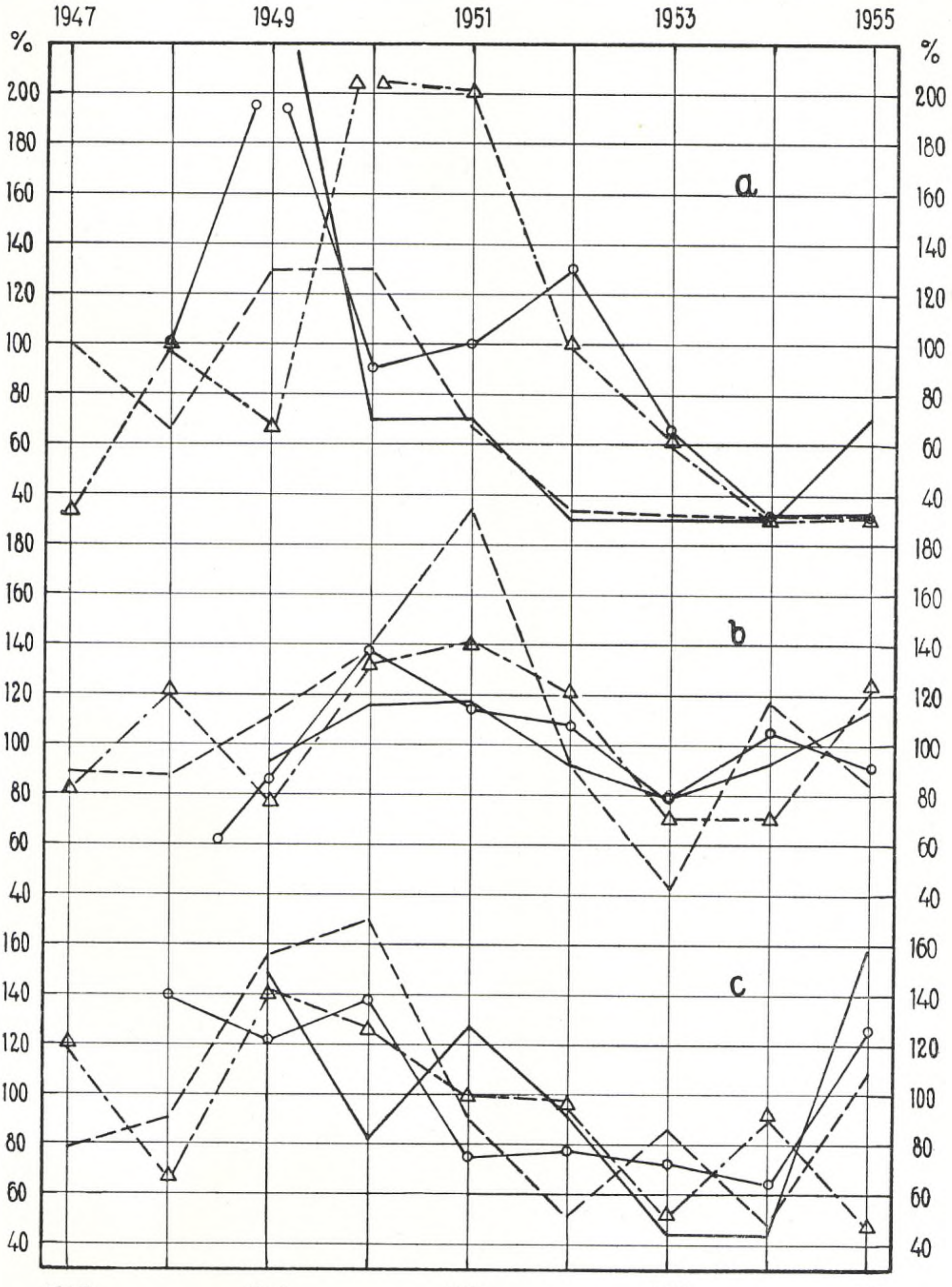

Fig. 15.

Abborre. Fångsten under a-, b- och c-perioderna (se texten) i °/₀ av medeltillförseln under dessa perioder.

Perch. Catch during the periods a, b, and c (see the text) expressed as percentages of the average supply during these periods.

(——— Stockholm; — — — Nyköping; o———o Norrköping; △—·—·—△ Oskarshamn.)

föreligger. De senare åren har fångsten under denna period överallt varit dålig. Fångsten under b-(lek)perioden, som i genomsnitt för olika områden växlar mellan 46 och 78 % av årsfångsten, uppvisar påtagliga likheter för samtliga områden med höga fångster 1950—51, delvis även 1952, och dåliga fångster 1953, delvis också 1949. En jämförelse med fig. 12 visar att stor överensstämmelse härvid råder med fångstkurvorna för gädda under samma period. Kurvornas förlopp åren 1954—55 är också detsamma både för abborre och gädda. Vad slutligen angår c-perioden märkes en genomgående nedgång i fångsterna från 1950 till 1954. För år 1955 kommer däremot för Stockholm-, Nyköping- och Norrköping-områdena en tydlig uppgång, fullt analog med förhållandena hos gäddan. Liksom för denna går däremot fångsten för Oskarshamn-området ned.

Allmänt kan om abborren sägas att förhållandena ej ligger så klart till som för gäddan, men att trots detta åskilliga likheter finnes. Så t.ex. är de goda årsfångsterna 1950—51 resp. de dåliga 1953 gemensamma för båda arterna. Och lekfångsternas likartade variationer inom de fyra områdena förlöper också i stort sett lika för gädda och abborre.

VII. Orsakerna till fluktuationer i gädd- och abborrfångsten

Av ovanstående har tydligt framgått, att fångsten av gädda och abborre vid Sveriges östersjökust uppvisar såväl mera långvariga som mycket kortvariga, ofta blott något år omfattande fluktuationer, att dessa fluktuationer i stort sett är mycket lika för de båda arterna, och att de även företer stora likheter för de olika länen. Vidare har visats att fångsten under lektiden, april—maj för gäddan, april—juni för abborren, uppgår till över en tredjedel resp. över hälften av hela årsfångsten, och att fångsten under senare delen av året, efter leken, endast omfattar 40 resp. 37 % av årsfångsten. Slutligen har framgått att större eller mindre fångster under lektiden eller under övriga delar av året i förhållande till hela årsfångsten uppträtt likartat utmed långa kuststräckor. Detta gäller främst gäddan, men har i viss grad också tillämpning på abborren. I det följande skall nu ett försök göras att undersöka vad orsakerna kan vara till dessa fluktuationer i fångsten.

Då här ovan talats om olika slags fluktuationer, nämligen långvariga och kortvariga sådana, bör framhållas att någon skarp gräns ej kan dragas mellan dem. Med de förra avses emellertid en följd av år, vars fångst ligger avsevärt över eller avsevärt under medelfångsten. Så t.ex. visar Stockholms län ett flertal goda fångstår 1920—30 och 1947—53 samt dåliga sådana 1931—45. Och Kalmar län har mycket tydliga sådana fluktuationer med goda fångster åren 1925—29 och 1939—51 samt lika dåliga fångster åren 1909—12, 1918—24, 1930—38 och 1952—55. Under dessa goda eller dåliga perioder förekommer emellertid ofta kortvariga fluktuationer på ett eller ett par år i bättre eller sämre riktning. Tydligast framträder dessa under den i Kalmar län goda flerårsperioden 1939—51. Mycket tydliga är sådana kortvariga fluktuationer också i Blekinge län samt under 1940-talet i Östergötlands län.

På samma sätt som det inte är möjligt att helt isärhålla dessa två slag av fluktuationer, är det ej heller möjligt att tydligt från varandra avgränsa de fakorer som kan tänkas orsaka desamma. Sålunda kan i båda fallen fiskeintensiteten och fångstens inriktning på olika fiskarter liksom även prisbildningen och efterfrågan spela in. Härtill kommer som påverkande faktor för de långvariga fluktuationerna beståndets växlande individrikedom under olika perioder, beroende på förekomsten av flera rika eller fattiga årsklasser, samt för de kortvariga, ofta årliga fluktuationerna faktorer som inverkar på själva fiskets bedrivande och på fiskens större eller mindre ansamling på fiskeplatserna.

A. *Överensstämmelsen i fluktuationerna hos gädda och abborre*

Innan övriga frågor närmare diskuteras, är det emellertid lämpligt att klarlägga orsakerna till den stora överensstämmelsen i fluktuationerna hos gäddans och abborrens fångstkurvor. Med stöd av vad som framkommit i föregående kapitel rörande fångstens säsongfördelning är en sådan överensstämmelse nu ganska förklarlig. Huvudfångsten av både gädda och abborre sker under en tämligen kort tid på våren och fisket utövas till stor del med samma redskap och av samma fiskare. Ett år med t.ex. givande gäddfiske i lekperioden gör, att man gärna fortsätter det mera intensiva fiskandet och då också får större fångst av abborre. Gäddfångsten bör, om detta är riktigt, fluktuera kraftigare än abborrfångsten. Och så är merendels även fallet. Då vidare gäddan och den större abborren är typiska fiskätare, är det naturligt att de båda uppträda i mängd på en plats, där tillgången på småfisk är god. Även detta gör att fångsten av dem ökar eller minskar samtidigt.

Framförallt förklaras, genom vad här anförts, likheter i de kortvariga fluktuationerna. Men också för samstämmigheten i de långvariga fluktuationerna spelar säkerligen huvudfångstens koncentrering till samma årstid en stor roll. Samtidigt måste man dock antaga att denna överensstämmelse också beror på likheter i beståndens storlek, d.v.s. deras individrikedom. Det måste annars vara svårt att förklara att under en följd av år med i stort sämre gäddfångster även abborrfångsten varit dålig, medan under de — bortsett från kortvariga fångstvariationer — givande gäddåren på 1940-talet också abborren givit goda fångster.

B. *Fiskeintensiteten och fångsten av olika fiskarter samt prisbildningen*

Fiskets omfattning kan under vissa omständigheter ha en högst påtaglig inverkan på beståndet. Under de båda världskrigen med åtföljande begränsning av fisket i Nordsjön och Östersjön förändrades sålunda i hög grad

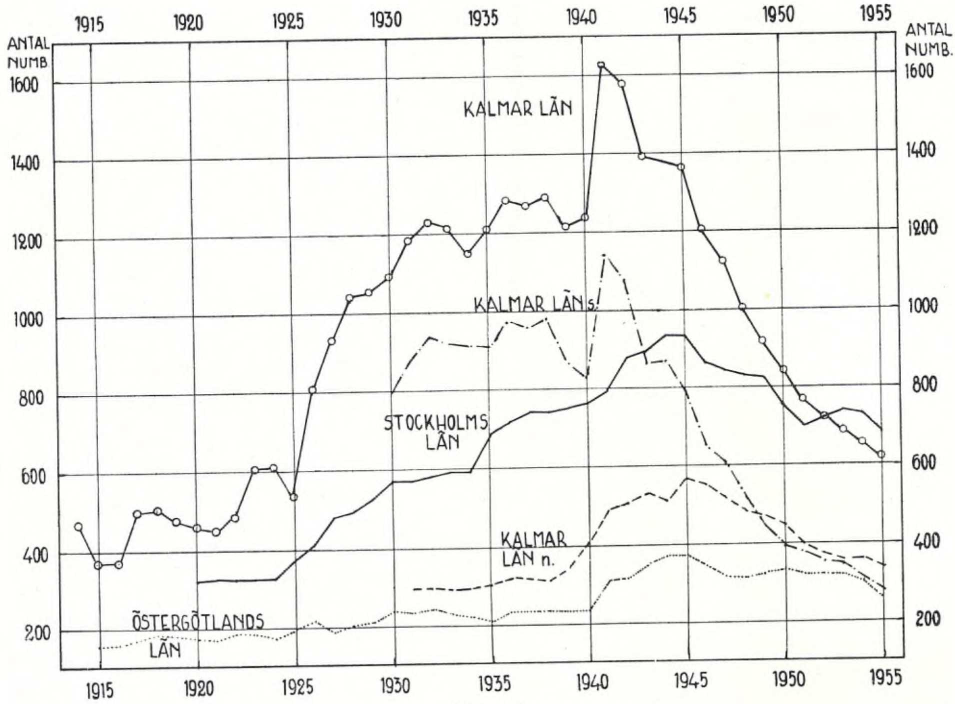

Fig. 16.

Antal yrkesfiskare under olika år i Stockholms, Östergötlands och Kalmar län.
Number of professional fishermen during different years in the provinces of Stockholm, Östergötland and Kalmar.

rödspättebestånden, så att mycket individrika men trögväxande sådana uppstod. Och i insjöar har stundom ett intensivt fiske medfört nedgång i avkastningen, t.ex. för siken i Bodensjön och för vissa sikarter i de stora sjöarna i Nordamerika. Dylika fall är dock ej så vanliga. Däremot föreligger ofta, ehuru icke alltid, ett visst samband mellan den tid de fiskande nedlägger på fångsten av en viss fiskart, d.v.s. fiskeintensiteten och fiskeansträngningen, samt själva fångstens storlek.

Vad angår fiskeansträngningen finns tyvärr i den officiella statistiken inga uppgifter över den tid, som ägnats ett visst slags fiske, eller det antal vittjningar som gjorts. Statistiken omfattar endast antalet fiskare och antalet redskap och båtar. Då även dessa uppgifter är av visst intresse, har på figurerna 16 och 17 grafiskt återgivits antalet yrkes- och binäringsfiskare i de tre viktigaste fångstlänen, Stockholms, Ösergötlands och Kalmar län. Vidare har på figur 18 inlagts kurvor för antalet använda ryssjor av olika typer, alltså det viktigaste fångstredskapet för både gädda och abborre, allt för åren 1915—1955.

I Stockholms län har både yrkes- och binäringsfiskarenas antal ökat med

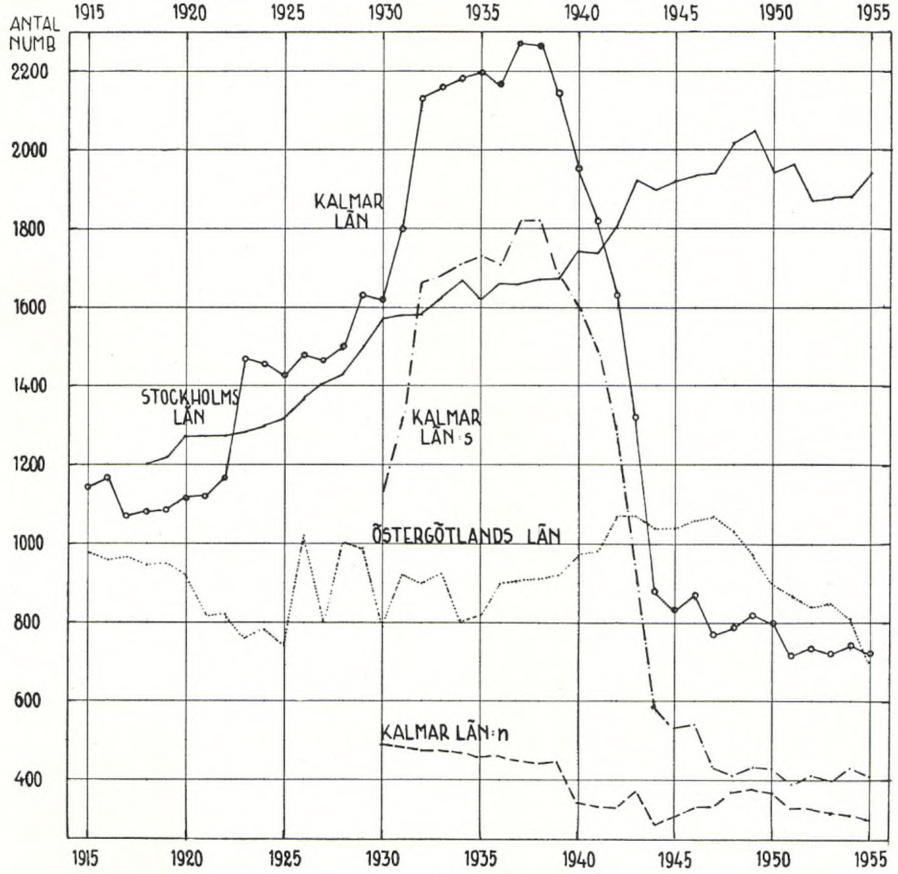

Fig. 17.

Antal binäringsfiskare under olika år i Stockholms, Östergötlands och Kalmar län.

Number of fishermen pursuing also another ocupation in the provinces of Stockholm, Östergötland and Kalmar.

kulmen omkring mitten av 1940-talet för yrkes- och mot slutet av samma årtionde för binäringsfiskarena. För yrkesfiskarena följer därefter en rätt avsevärd minskning. Östergötlands län visar också för yrkesfiskarena en jämn men mycket svagare ökning, även här kulminerande under 1940-talet. Kalmar län utmärkes av en från och med år 1925 synnerligen kraftig ökning av antalet yrkesfiskare med toppen de första 1940-åren. Sedan följer en mycket markerad, stadig nedgång. De efter år 1930 inlagda kurvorna för norra och södra länsdelen var för sig visar att det särskilt är den senare som företer den stora nedgången. Växlingarna i antalet binäringsfiskare visar stora likheter med yrkesfiskarena, men nedgången börjar här tidigare.

En jämförelse med figurerna 2 till 6 visar att fångsterna överallt varit störst under 1940-talet. I någon mån har troligen härtill bidragit det samma

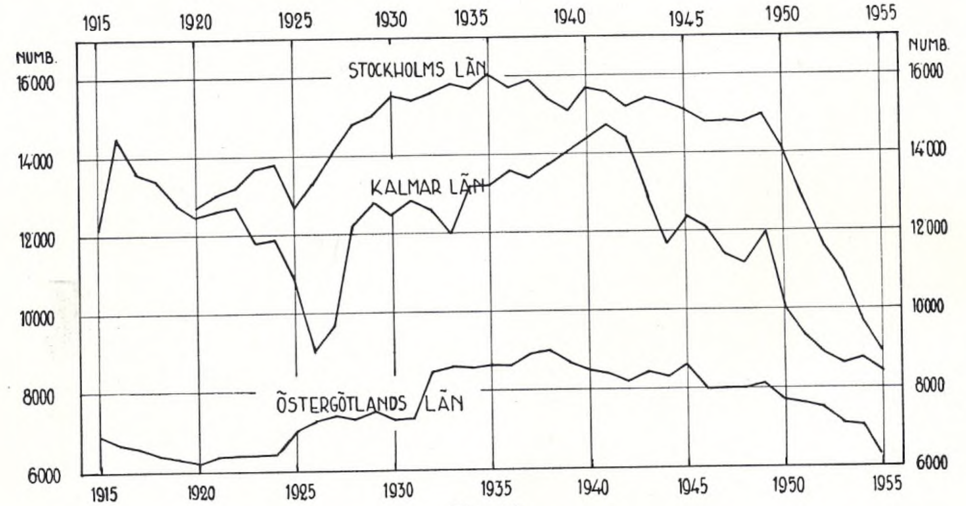

Fig. 18.

Antal ryssjor och bottengarn under olika år i Stockholms, Östergötlands och Kalmar län. *Number of fyke-nets and traps during different years in the provinces of Stockholm, Östergötland and Kalmar.*

tid ökande antalet fiskande. Å andra sidan var detta antal lågt under de båda goda fångstperioderna omkring åren 1915 och 1927. Och den rätt jämna ökningen i antalet fiskare under 1920 och 1930-talen motsvarades av låga fångstsiffror. En omständighet, som i detta sammanhang ej får förbises, är den större ansträngning som sannolikt nedlades på fisket under krigsåren 1915—18 och 1940—45, trots att då antalet fiskande genom inkallelser var mindre än vanligt. Det är möjligt att också detta medfört en höjning av avkastningen och bidragit till de goda fångsterna i flertalet län av både gädda och abborre. Å andra sidan kan härigenom ej förklaras de i samtliga län särskilt för gädda mycket givande fångståren i mitten av 1920-talet.

Av figur 18 framgår att ryssjor användes mest i Stockholms län. I samtliga tre län var antalet störst under 1930-talet och början av 1940-talet. Under de senaste 10 åren nedgick antalet, mest i Stockholms län. Antalet använda ryssjor ger inte belägg för något närmare samband med fångstmängden. För t.ex. Stockholms län sammanfaller snarast dåliga fångstår med den period, då antalet ryssjor var störst. Och under de givande åren på 1920-talet och omkring 1950 var antalet ryssjor mindre än på 1930-talet. I Kalmar län slutligen börjar den kraftiga nedgången i ryssjemängden ungefär samtidigt med att de bästa fångståren inträder. Nämnas bör att en granskning av i statistiken förefintliga uppgifter över antalet använda nät icke heller givit stöd för att denna redskap varit en bidragande orsak till fångstfluktuationerna för gädda och abborre. Nät användas dessutom i långt högre grad än ryssjor för fångst även av andra fiskarter.

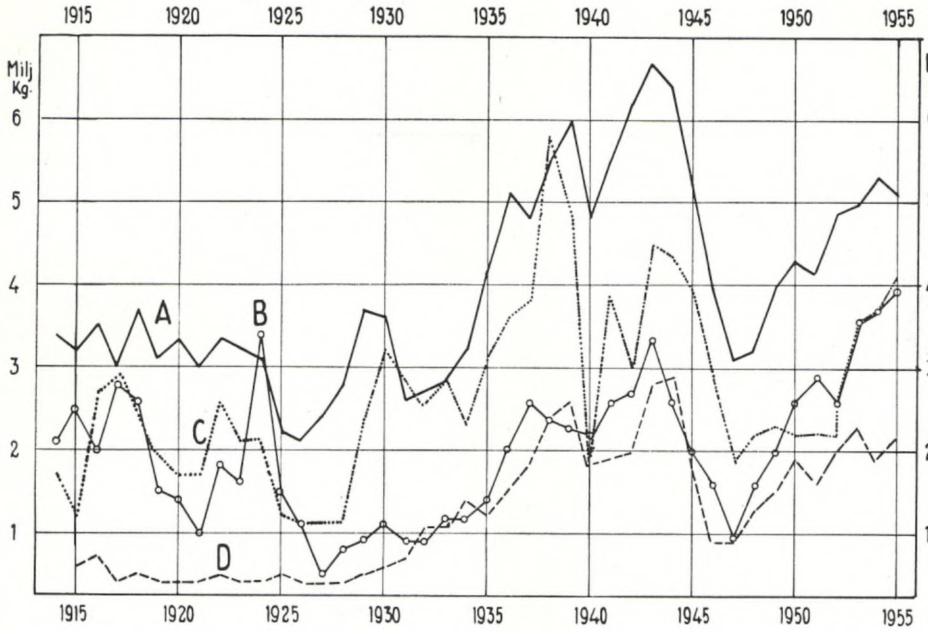

Fig. 19.

Årsfångsten av strömming i (A) Stockholms, (B) Östergötlands, (C) Kalmar och (D) Södermanlands län.

Annual catch of Baltic herring in the provinces of Stockholm, Östergötland, Kalmar and Södermanland.

Amerikanska undersökningar har visat (Hile, Lunger och Buettner 1953, Smith och Krefting 1954) att stark intensifiering av fisket efter en viss art i samband med rik tillgång på densamma ibland medfört ökad fångst också av någon annan art, vare sig beståndet av denna varit särskilt stort eller så icke varit fallet. Det motsatta kan emellertid också inträffa. Sålunda uppgives ibland av fiskare, att de ett år ägnar sig så flitigt åt fångsten av en viss fiskart, att fisket efter en annan art mera försummas. Ett dylikt fall uppger även fiskerikonsulent Westling från Åland. Där bedrevs under mitten av 1940-talet, då strömmingen lämnade mycket goda fångster, intet större gäddfiske. När strömmingstillgången minskade åren 1947—49 övergick man däremot mera till sådant. Mycket stora gäddfångster gjordes då på det under de tidigare åren endast svagt beskattade beståndet. Efter några år minskade gäddfångsten, men höll sig därefter som ovan nämnts mera jämn.

För att undersöka om möjligen fisket efter andra arter än gädda och abborre har inverkat på fångsten av dessa har på figurerna 19 och 20 inlagts fångstkurvor för de viktiga arterna strömming och torsk inom de tre för gädda och abborre mest betydande länen samt dessutom på figur 21 fångst-

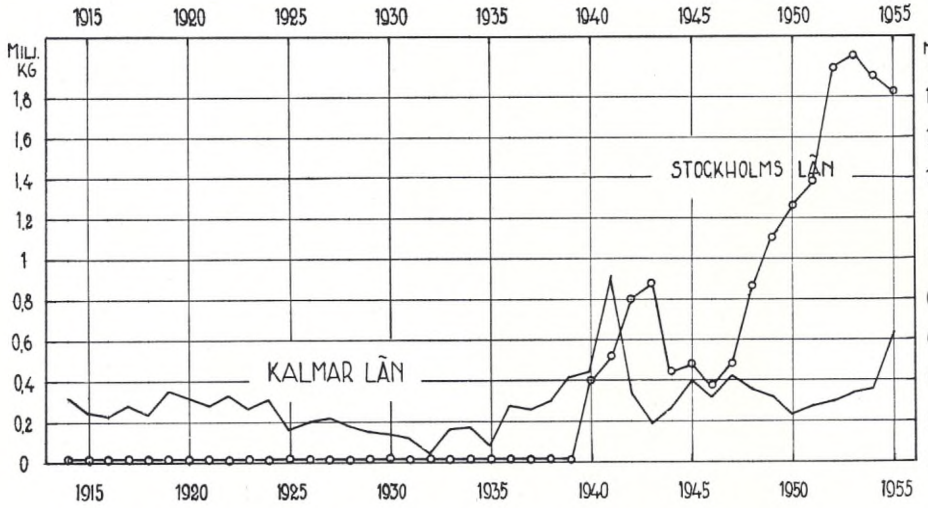

Fig. 20.

Årsfångsten av torsk i Stockholms och Kalmar län.

The Annual catch of cod in the provinces of Stockholm and Kalmar.

kurvor för samtliga viktigare fiskarter i Kalmar läns södra del. Strömmingsfångsten i de tre ovannämnda länen har fluktuerat mera oregelbundet fram till mitten på 1930-talet. Då har en kraftig ökning ägt rum. Med större eller mindre nedgång har fångstkurvan sedan, i varje fall för Stockholms län, legat högt under närmare 10 år framåt. Efter en allmän nedgång omkring 1947—48 har åter en ökning i fångsten ägt rum under 1950-talet. Därest såsom under 1940-talet på Åland ett mer eller mindre intensivt strömmingsfiske skulle ha inverkat minskande på den tid som ägnats gädd- och abborrfisket, borde fångstmängderna här ha alternerat. Snarare föreligger nu en viss likhet, såtillvida som i båda fallen de bästa fångstperioderna infallit under 1940-talet. De goda gäddfångsterna omkring åren 1914—1915 och 1926—1928 motsvaras möjligen i senare fallet av en viss nedgång i strömmingskurvan, medan denna i förra fallet endast uppvisar smärre variationer.

Den näst strömmingen viktigaste fiskarten i dessa län är torsken. Av figur 20 framgår att inte heller här något annat samband kan påvisas med gädd- och abborrfångsten än att också torskfångsten ökar kraftigt under 1940-talet. Detta gäller särskilt Stockholms län, och denna ökning fortsätter här ännu mera under 1950-talet. Nämnas kan att även laxfisket i Östersjön visade ett mycket stort uppsving under 1940-talet. Delvis bedrives detta fiske av sådana yrkesfiskare, som inte ägnar sig åt gädd- och abborrfiske, men i andra fall utövas det av samma personer.

Det är också av intresse att se om inriktningen på andra fiskarter har något samband med de kortvariga fluktuationerna i fångsten av gädda och

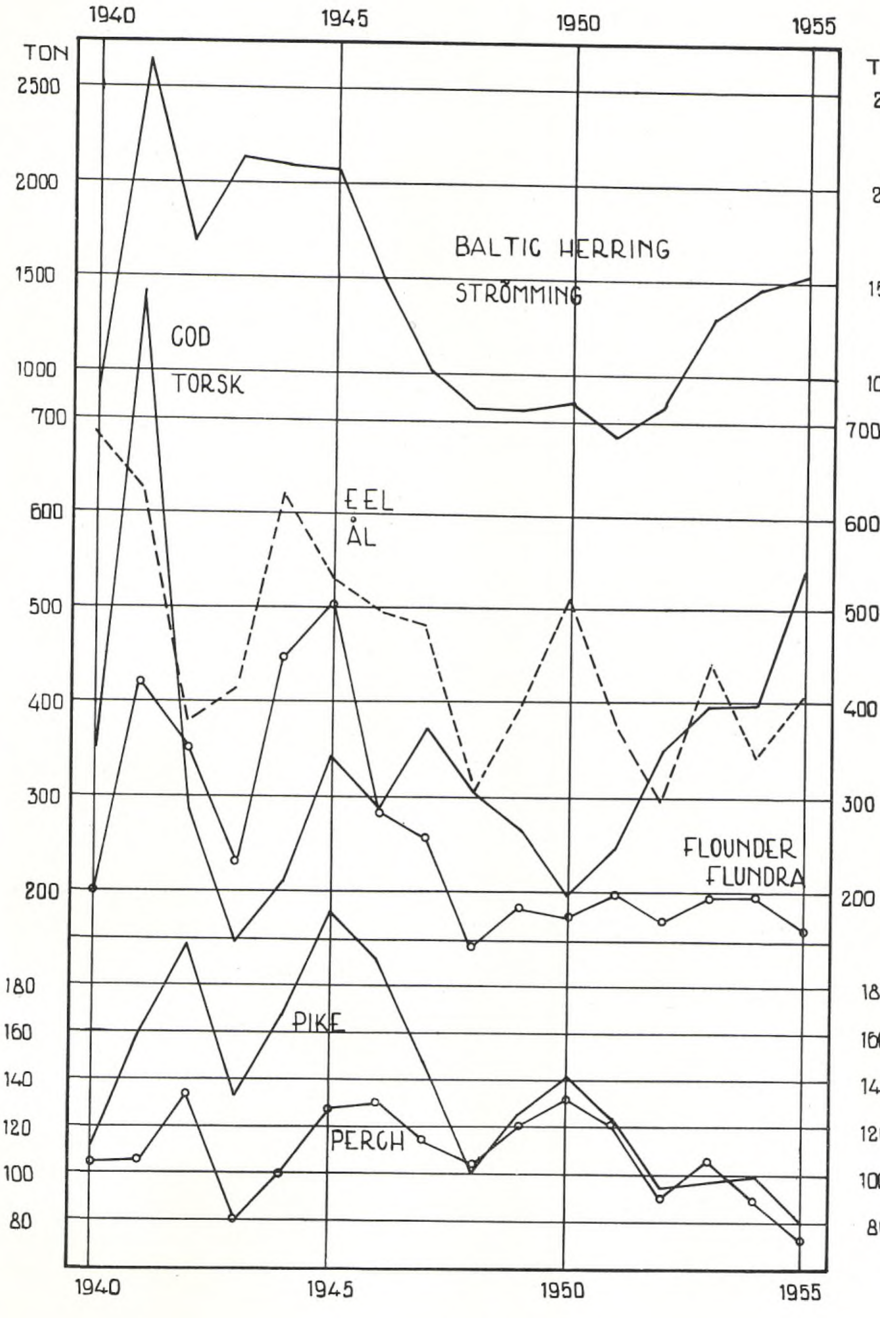

Fig. 21.

Årsfångsten av strömming, torsk, flundra, ål, gädda och abborre i Kalmar läns södra del.

The annual catch of Baltic herring, cod, flounder, eel, pike and perch in the southern part of province of Kalmar.

abborre. Härför har valts Kalmar läns södra del, som ju uppvisade särskilt tydliga dylika fluktuationer under perioden 1939—1950. På figur 21 har inlagts fångstkurvor för icke bara strömming och torsk utan även för de i detta län betydande arterna ål och flundra. Trots stora avvikelser visar dessa fångstkurvor för flera år en viss överensstämmelse. Sålunda gav år 1941 goda fångster av samtliga fyra arter utom gädda, där fångsten var medelmåttig. Under år 1945 var strömmingsfångsten ej särskilt hög, ehuru över medelfångst. Men såväl torsk och ål som flundra och gädda gav höga fångster. Frånsett ålen var utbytet av strömming, torsk, flundra och även gädda dåligt under år 1940. Samma gäller torsk, ål, flundra och gädda under år 1943. Och år 1948 gav dåliga fångster av både strömming, ål, flundra och gädda. För denna länsdel har även, utan att de inlagts på figuren, jämförts fångstsiffrorna för de här relativt viktiga arterna id och mört. Sinsemellan visar fångsten av dessa mycket likartade fluktuationer. Fångsten av dem båda är också hög under de rätt goda gäddåren 1941—42, sjunker som hos gäddan under år 1943 och stiger åter något under de rätt givande gäddåren 1945—46.

För att ytterligare undersöka om en sådan samstämmighet i fångsten av flera arter framträder även på andra håll har en granskning skett dels av fångsterna i Östergötlands län under åren 1940—1950, då gäddfångsten fluktuerat mycket starkt, dels för åren 1920—1930 i Kalmar län, som under den perioden uppvisar en mycket kraftig fångsttopp för gädda med kulmen år 1927. Utan att i detalj ingå härpå kan anföras att i Östergötlands län för åren 1940—47 fångstkurvorna för torsk och flundra dels följer varandra, dels även visar stor likhet med motsvarande kurvor för Kalmar län, speciellt med toppar åren 1941 och 1945 och sänkor åren 1940 och 1943. Gäddfångsten låg däremot här högt under åren 1940 och omkring 1945 men lågt under åren 1942—43, varför någon större överensstämmelse här ej föreligger. Beträffande Kalmar läns höga gäddfångst år 1927 har denna sin motsvarighet samma år i en ovanligt hög ålfångst. Även torsk och flundra samt braxen och id uppvisade detta år högsta fångst i förhållande till närmast föregående och efterföljande år.

Det är givet att nu påvisade samstämmighet i fångsten av inte bara gädda och abborre utan för flera år också av andra viktiga fiskarter icke kan tillskrivas någon full positiv korrelation. Härför äro avvikelserna under andra år alltför stora. Det är emellertid å andra sidan tydligt, att teorien om alternerande fisken icke har något stöd i den föreliggande fångststatistiken.

Orsaken till den i flera fall påtagliga överenskommelsen kan, därest den icke är helt slumpmässig, givetvis icke ligga i variationer i individmängden hos de berörda arterna, och icke heller i faktorer, som medfört olika ansamling av dem på fångstplatserna. Härtill är deras biologi och fångstsätt alltför olika. Enda förklaringen synes vara, att under vissa år ett större antal av de i statistiken uppgivna fiskarena ägnat sig åt fiske än under andra år, eller

Tabell 7. Medelpris i öre per kg för gädda och abborre. — *Average price in öre per kilogramme for pike and perch.*

År	Gädda	Abborre	År	Gädda	Abborre
1940	115	58	1948	206	77
1	170	89	9	197	73
2	209	121	1950	195	74
3	223	112	1	202	76
4	205	84	2	219	85
1945	208	78	3	228	87
6	191	64	4	231	87
7	190	63	1955	232	86

att med samma antal fiskare den s.k. fiskeansträngningen växlat. Man kommer då in på sociala och ekonomiska frågor, som är svåra att överskåda. Här må endast prisbildningen nämnas.

Priset på en viss fiskart växlar rätt mycket och kan indirekt inverka på lusten att bedriva fångst av densamma. Sålunda bör under ett år med höga priser fiskaren lockas till större ansträngning vid fiskets utövande och tvärtom. Men priset är samtidigt beroende av fångstmängden. Det sjunker vid stor tillförsel och motverkar då den förstnämnda tendensen. I tabell 7 har införts medelpriser per år för gädda och abborre under åren 1940—1955. De högsta priserna förekom under åren 1942—45, 1948 och särskilt för gädda även de senaste åren fr.o.m. år 1952. Åren 1943, 1948 och 1952—55 motsvaras emellertid av låga fångster av såväl gädda som abborre, och toppfångsterna 1941—42, 1945—46 och 1950—51 har delvis gjorts under år med låga priser på dessa fiskslag. Någon korrelation mellan högre priser samt ökad fiskeintensitet och större fångster eller tvärtom föreligger sålunda ej.

Vad nu anförts om fiskets intensitet och dess inriktning på olika fiskarter har inte givit belägg för att man häri kan finna någon allmängiltig förklaring till fluktuationerna i gädd- och abborrfisket. Tydligt är emellertid att samtliga för de ifrågavarande länen viktigaste fiskarterna gav de största fångsterna under den period på 1940-talet, då även antalet fiskare nådde sin kulmen. I vilken grad de goda fångsterna av gädda och abborre berodde på denna ökade fiskeintensitet, eller på att fiskbestånden var särskilt rikliga, eller på bådadera, är ej möjligt att avgöra. Vidare är tydligt att vissa år givit goda, andra år åter dåliga fångster av flera arter, och att detta sannolikt sammanhänger med variationer i fiskeansträngningen under olika år.

C. *Årsklasserna och beståndet*

Ett fiskbestånds större eller mindre riklighet beror främst på årsklassernas individrikedom. Redan en enda mycket rik årsklass av sill eller strömming har ökat avkastningen inom stora havsområden under en följd av år.

Samma sak gäller t.ex. laxen. Och flera, år efter år eller med kortare uppehåll följande goda, resp. fattiga årsklasser av en viss fiskart måste för en längre period ge upphov till ett rikare eller fattigare bestånd, som då också i viss grad, oberoende av andra faktorers påverkan, återspeglas i bättre eller sämre fångster.

Årsklassernas dimensionering kan i sin tur tänkas bero på a) lekbeståndets storlek, b) klimatiska faktorer som påverkar leken, rom- och yngelutvecklingen, tillgången på föda för ynglet samt förekomsten av fiender och därmed sammanhängande överlevnad, c) odling och utplantering av yngel eller större ungar.

a. Lekbeståndets storlek

Ett flertal fiskeribiologiska undersökningar och försök såväl i Sverige som utomlands har visat att i allmänhet antalet lekande fiskar har ett ganska litet inflytande på den nya årsklassens storlek. Ett tämligen fattigt lekbestånd kan ge upphov till en mycket rik ny årsklass. Och motsatt har ofta mycket rika lekbestånd åtföljts av dåliga årsklasser.

Undersökningar över gäddans lek (MONTÉN 1948, 1949, SVÄRDSON 1945, 1946) har visat att rommen avläggs i små portioner på skilda platser inom ett större lekområde, och att även vid ett mycket intensivt ryssjefiskande på lekplatserna en stor del gädda undgår fångst. Man kan därför säkerligen utgå från att, utom i enstaka undantagsfall, en fullt tillräcklig rommängd finnes för att, om förhållandena i övrigt är gynnsamma, ge upphov till en rik årsklass av gädda. Detta gäller i än högre grad om abborren. Lekbeståndens storlek har därför säkerligen ej haft någon större inverkan på uppkomsten av olika rika årsklasser.

b. Klimatiska faktorer, föda, fiender

Resultatet av leken och dimensioneringen av en ny årsklass beror säkerligen främst på faktorer som gynnar eller försvårar rommens och ynglets utveckling eller som orsakar större eller mindre tillgång på föda för ynglet eller som påverkar förekomsten av rom- och yngelätande djur. Det kan antagas, att dylika faktorer har en tämligen likartad inverkan både på gäddans och abborrens fortplantning, trots olikheterna ifråga om det nykläckta ynglets beteende. Härav följer att ganska likartade växlingar kunna uppstå i de båda beståndens riklighet. Den olika tillväxthastigheten och olika fångståldern hos gädda och abborre spelar ingen större roll, när det gäller dessa längre perioder av rikare eller fattigare bestånd, enär fångståldern då delvis måste sammanfalla. Vid liknande undersökningar i Amerika (HILE, LUNGER, BUETTNER 1953) har man också funnit att rika årsklasser av flera arter uppstått samtidigt. I vissa fall har detta gällt gös och abborre (SMITH och KREFTING 1954) och medfört samtidiga fluktuationer i fångsten. Abborrens fångstålder är i Nordamerikas sjöar avsevärt lägre än hos oss (HILE and JOBES 1941) och sammanfaller ungefär med gösens och gäddans.

De faktorer, som nu närmast kommer ifråga, torde vara tidpunkten för leken, vattentemperaturen och vattenståndet under rom- och yngelstadiet samt vindförhållandena. En mild vinter med tidig vår och hög vattentemperatur i fortsättningen gynnar rommens och ynglets utveckling och medför en rik tillgång på plankton och andra för ynglet begärliga näringsdjur. Dessutom bör även uppstå goda årsklasser av mört, braxen, id m.fl. vårlekande fiskarter, som ökar tillgången på föda för de större ungarna av gädda och abborre. En sen och kall vår har en motsatt inverkan. Särskilt blir detta fallet, om leken inträffar mycket sent och åtföljes av en köldperiod. Det är heller ej omöjligt, att en mycket sen vår med exceptionellt låga temperaturer ända in i juni månad kan göra att lek uteblir hos en del exemplar. SEGERSTRÅLE (1932, 1948) har påvisat detta såväl hos abborre som hos braxen från Finlands skärgårdar. Och ROLLEFSEN (1949) har framhållit att den lekmogna torsken uteblir från mycket stora havsområden, om vattentemperaturen är för låg.

I insjöarna sjunker vattenståndet ofta efter gäddleken. Resultatet av densamma står också, som bland annat CARBINE (1943) och MONTÉN (1949) visat, i visst samband med storleken av denna sänkning. Vid kusterna förekommer också variationer i vattenståndet, framförall beroende på meteorologiska faktorer av större omfattning (BERGSTEN 1950, 1955). De blir därför mycket likartade utmed långa kuststräckor. I allmänhet är då vattenståndet lägre på våren än under andra årstider, och månaden maj uppvisar normalt det lägsta medelvattenståndet. Skillnaderna i medelvattenståndet mellan olika dagar och månader eller mellan olika år uppgår i allmänhet ej till mera än 10 à 20 cm, ibland dock upp till 30 à 40 cm. Ofta beror detta på speciella vindar, vilkas inverkan på ostkustens vattenstånd dock är mycket mer komplicerat än vid västkusten (BERGSTEN 1955). För att närmare åskådliggöra dessa förhållanden har i figur 22 inlagts vattenståndskurvor för de senaste femton åren för månaderna april, maj och juni. Detta har ansetts särskilt befogat, enär dylika diagram över vattenståndsförhållandena vid kusten ej synas föreligga i den tillgängliga litteraturen. Siffrorna är hämtade från S.M.H.I:s årsböcker och avse Landsort.[1]

Vattenståndet vid kusterna skiljer sig alltså rätt påtagligt från vattenståndet vid sjöarna, där ju under våren vanligen råder ett stadigt, mera långsamt sjunkande högvattenstånd. Å andra sidan spelar vattenståndet ej så stor roll vid kusterna. Som tidigare framhållits leker endast en del gädda på grunt vatten, medan den övriga delen leker på ett djup av en halv till ett par m. Endast i förra fallet, som gäller långgrunda, växtklädda vikar i

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[1] Landsort har valts såsom typiskt för Ostkusten. Närmaste station söderut med mareograf är Kungsholmsfort i Blekinge. Vattenståndskurvornas förlopp vid dessa båda stationer har i viss mån varit likartat.

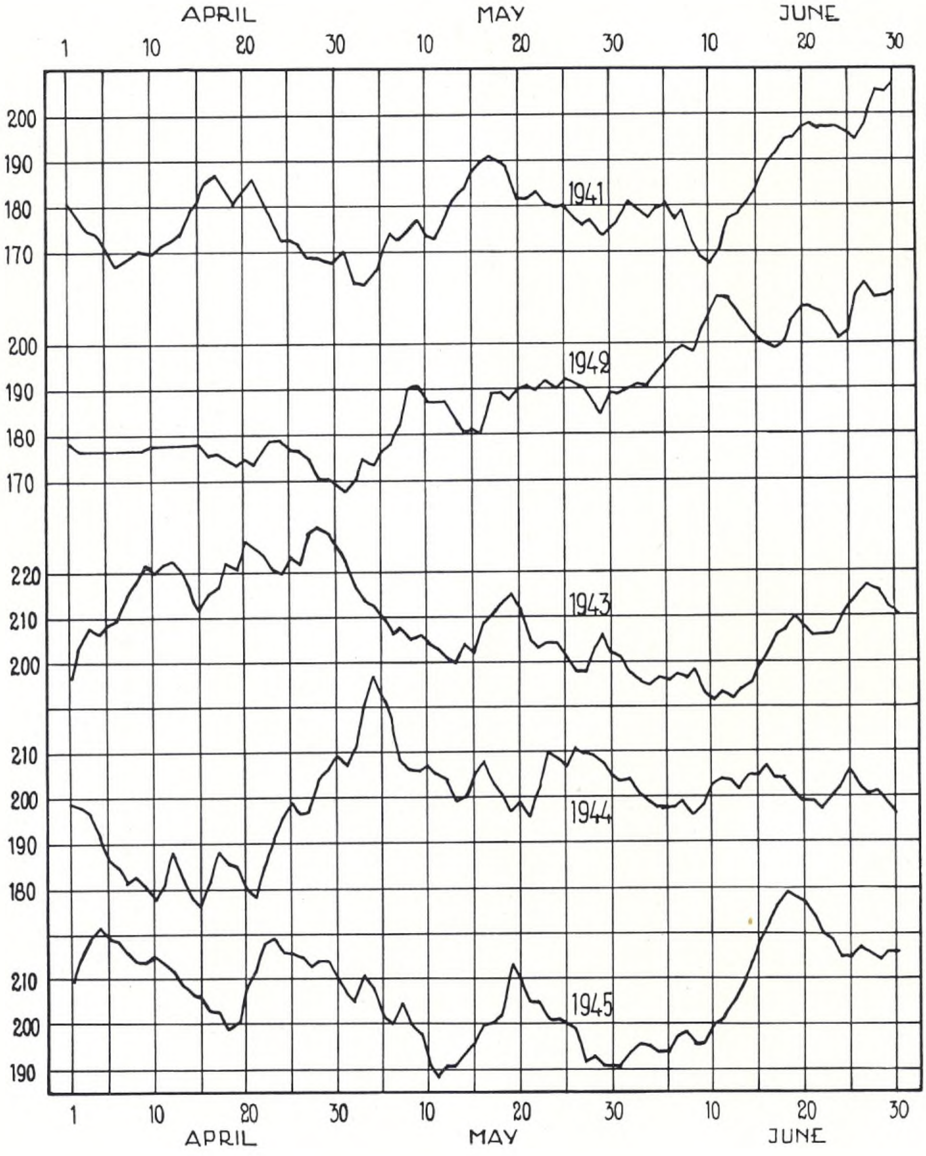

Fig. 22 a.

De dagliga medelvattenstånden vid Landsort under månaderna april, maj och juni åren 1941—1955. (Enligt S.M.H.I:s efter visst indextal beräknade värden i cm.)

The daily mean water-level at Landsort during the months April, May, and June of the years 1941—1955.

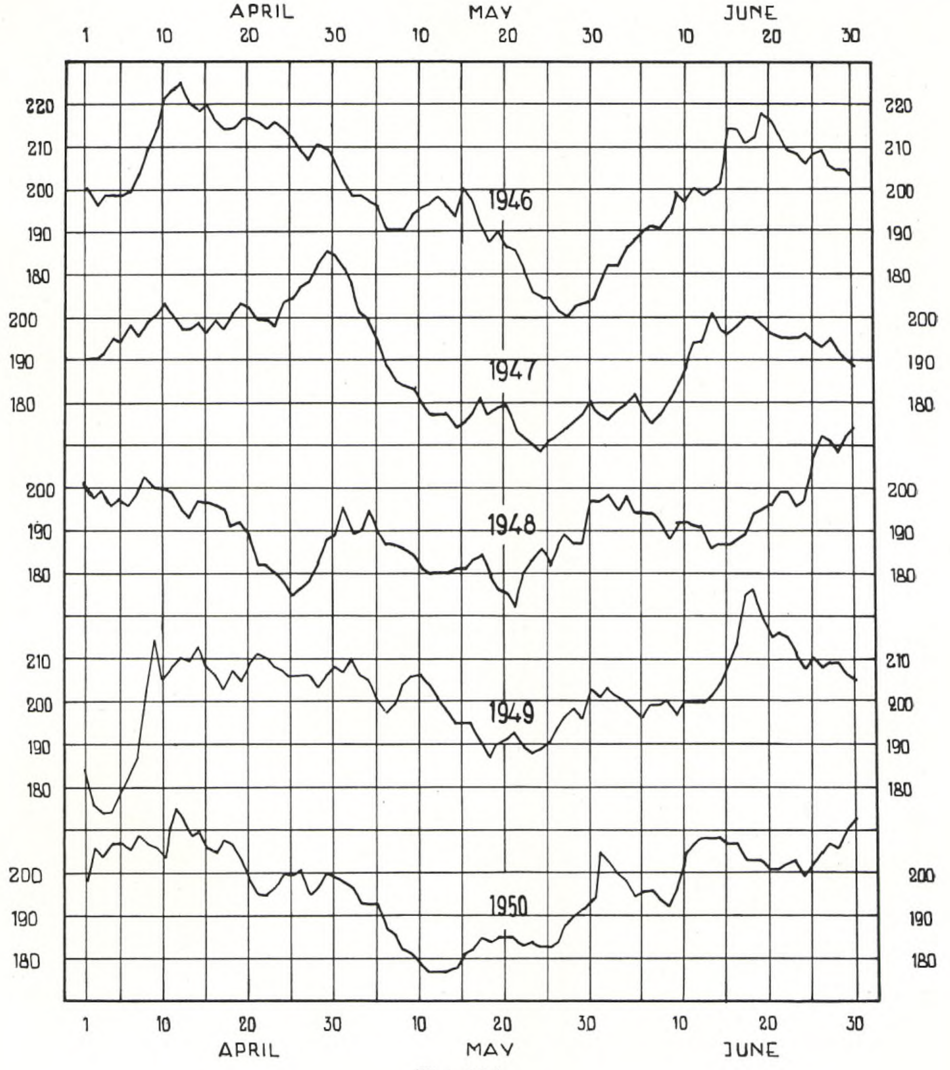

Fig. 22 b.

innerskärgårdarna, kan en sänkning av vattenståndet på 20 à 30 cm medföra torrläggning av rom och yngel. De djupare lekplatserna berörs givetvis icke härav.

Vad angår vindens inverkan må anföras att Järvi (1942) påvisat visst samband mellan stormig väderlek och felslagna årsklasser av siklöja. Genom det häftiga vågsvallet skulle ynglet spolas upp på stränderna och dödas. Det synes ej omöjligt att även gädd- och abborrynglet kan utsättas för sådan påverkan. Det på vegetationen fastsugna gäddynglet kan vid häftiga vågrörelser slitas loss, och det driver kanske då samman med det ytterst späda och ömtåliga abborrynglet in mot stränderna.

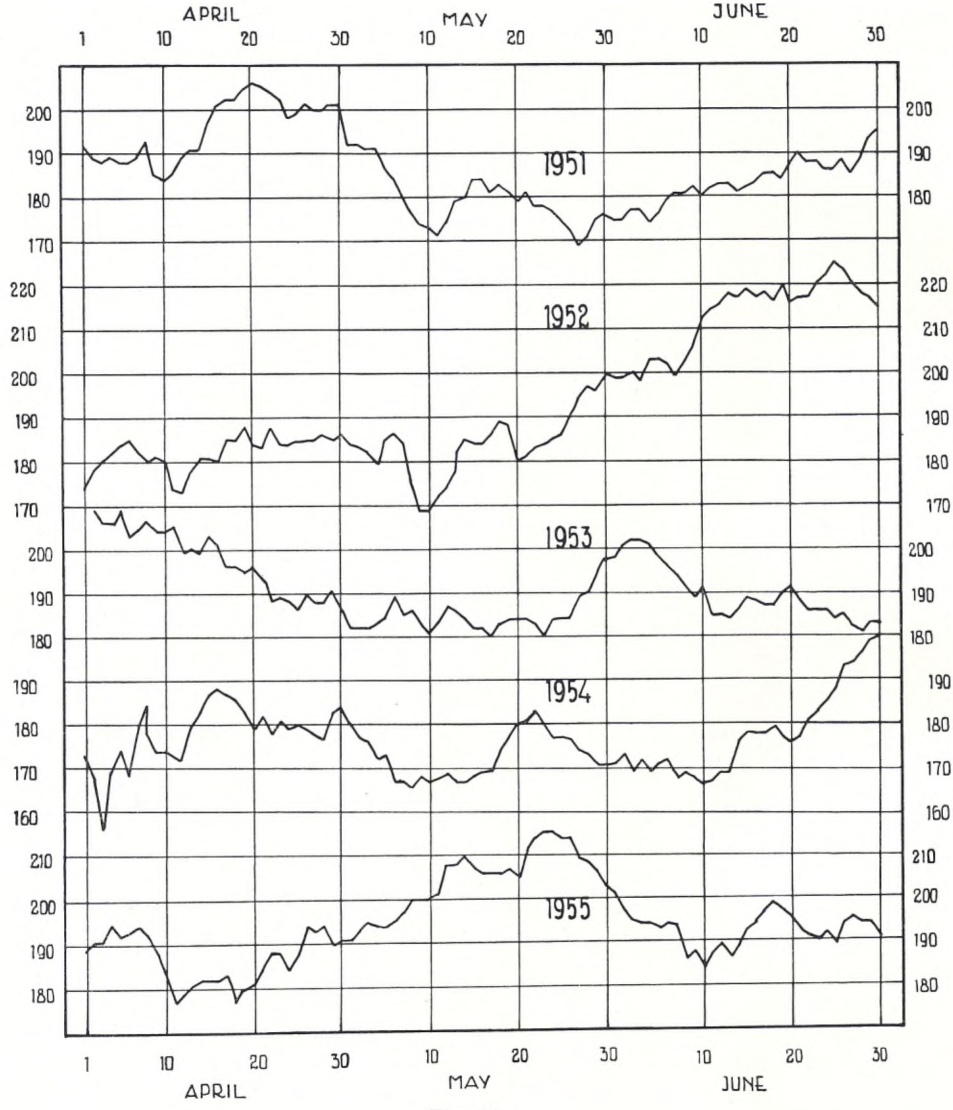

Fig. 22 c.

Uteslutet är ej heller att de lösslitna tångmassor, på vilka gäddan som förut nämnts ibland leker, vid hårda vindar spolas upp på stränderna, så att både anhäftande rom och yngel omkommer. Att därför lugna väderleksförhållanden är bättre för rom- och yngelutvecklingen än storm och oväder måste anses ganska säkert.

Såväl rom som yngel av flertalet fiskarter är utsatt för angrepp från olika fiskarter och andra vattendjur. Ifråga om gäddan har detta särskilt påvisats av Montén (1948) och Tägtström (1946). Den större eller mindre förekomsten av dylika fiender på lek- och uppväxtplatserna är beroende av i stort samma faktorer, som inverkar på gädd- och abborr-rommens och -ynglets utveckling, och dessa faktorer har då ofta samma positiva eller negativa verkan. I många fall motverkas därför ett gott fortplantningsresultat och god tillgång på föda av en samtidigt rikare förekomst av fiender. Överlevnaden av en viss årsklass påverkas i hög grad av denna faktor.

Därest de förutnämnda goda fångståren omkring 1914—15, 1926—27, under 1940-talet och 1950—51 orsakats av förekomsten av rika årsklasser särskilt av gädda, borde dessa med hänsyn till fångståldern ha tillkommit 4 à 6 år tidigare. Och de dåliga fångstperioderna omkring år 1920, i början av 1930-talet och under de senare åren bör ha orsakats av ogynnsamma förhållanden för fortplantning och yngelutveckling några år tidigare. En undersökning har nu företagits rörande ett flertal klimatologiska faktorers förlopp under lek- och yngelmånaderna april, maj och juni för åren 1919—1955. De prövade faktorerna är följande: lufttemperaturen för Stockholm och Kalmar (S.M.H.I:s årsböcker), vattentemperaturen vid fyrskeppen Stora Björn och Ölands rev (Fiskeristyrelsens fyrskeppsobservationer m.fl.), istäckets varaktighet inom Östersjöområdet[1] (JURVA 1952) samt medelvattenståndet under vårmånaderna vid Landsort (S.M.H.I:s årsböcker och BERGSTEN 1925). Också nederbörds- och vindförhållanden ha uppmärksammats. Vissa av dessa faktorers fluktuationer ha grafiskt återgivits i figur 23. Överst i densamma har inlagts fångstkurvan för gädda, efter en genomsnittlig fångstålder av 5 år, förskjuten 5 år bakåt.

Kurvorna för istäckning samt vatten- och lufttemperaturer visar sinsemellan viss samstämmighet. En sträng vinter sammanfaller oftast med låga temperaturer under vårmånaderna och alltså med en sen vår och tvärtom. Detta håller dock icke alltid streck. De hårda vintrarna 1926 och än mera 1947 åtföljdes av en tämligen hastig uppvärmning, och den milda vintern 1927 av en relativt sen vår. Framhållas må att enligt KOCZY (1954) medeltemperaturen i östersjövattnet ökat från de tidigare åren på 1920-talet till senare 1930-åren för att under 1940-talet hålla sig mera jämn. Följande siffror för medeltemperaturen under olika 6-årsperioder vid fyrskeppet Stora Björn kan anföras som exempel.

	April	Maj	Juni
1923—28	1,5	3,8	7,6
1929—34	1,7	4,1	8,8
1935—39	1,9	4,6	9,8
1946—52	1,8	4,5	9,6

Vad angår vattenståndet motsvarades de sena vårarna 1940—42 ävensom 1923 av i början ovanligt lågt vattenstånd, men dylikt förekom också åren

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[1] Siffrorna ange i 10.000 km² den istäckta arealen av Östersjöns till 420.000 km² uppskattade yta.

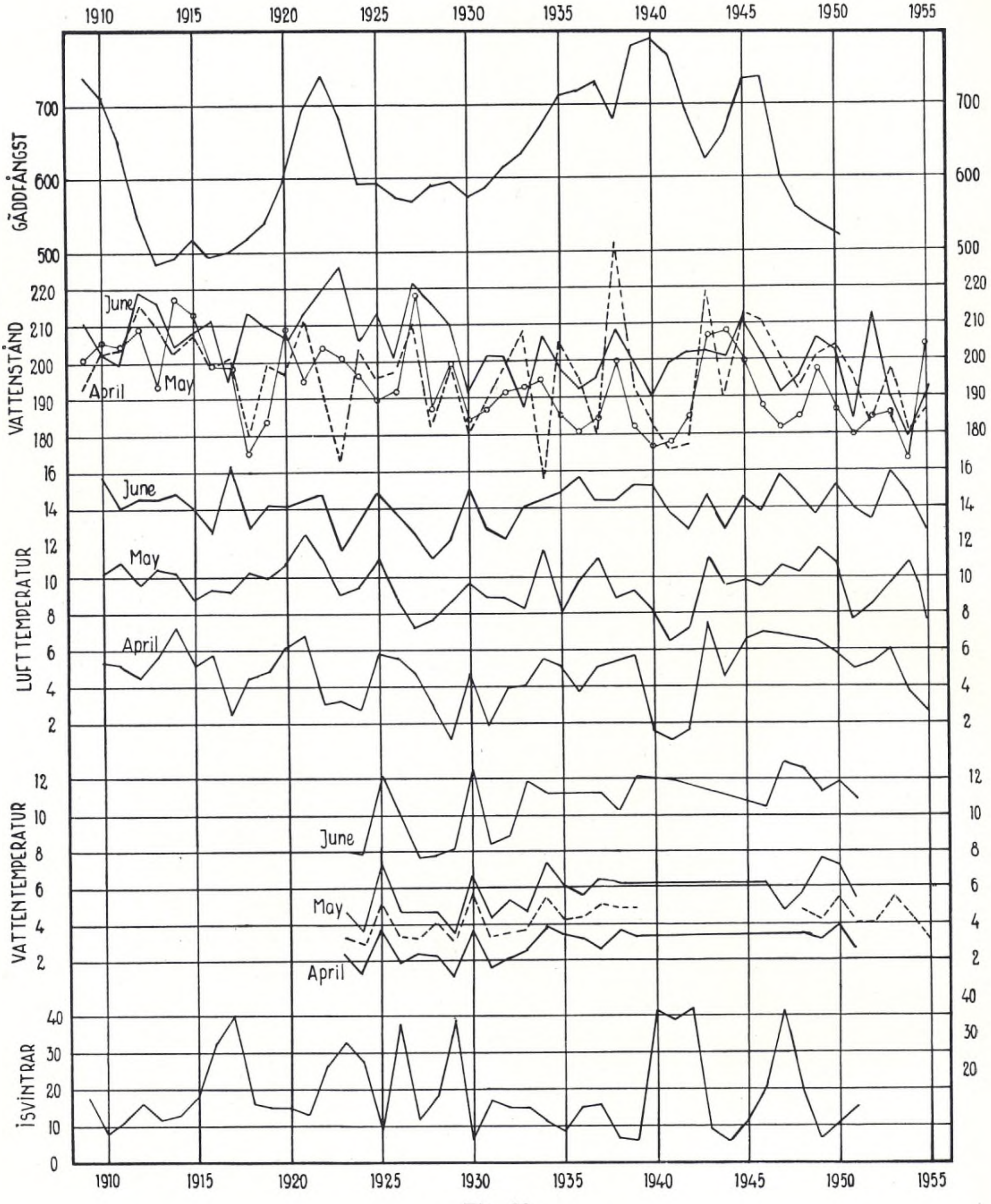

Fig. 23.

Grafisk framställning av vissa klimatförhållanden vid östersjökusten under åren 1909—1955. Isvintrar enligt Jurva (se sid. 49) medelvattentemperatur i °C vid Ölands rev (———) och Stora Björn (— — —), medellufttemperatur i °C vid Kalmar, vattenstånd i cm enligt S.M.H.I:s efter visst indextal beräknade värden samt gäddfångsten i ton, förskjuten fem år tillbaka.

Graphic representation of certain climatic conditions along the Baltic coast during the years 1909—1955. Ice-winters (Jurva), mean water and air temperatures in °C, water-level and catch of pike, 5 years back.

1918 och 1934 i samband med tidig vår. Och under de sena vårarna 1917 och 1929 var vattenståndet högt.

Till vindförhållandena har hänsyn ej tagits. På grund av lekområdenas skiftande läge i väderstreck, i utsatthet för vindar, i djup etc. måste särskilt vinden få en ännu mera skiftande inverkan inom olika områden än de förutnämnda faktorerna.

Här berörda oregelmässigheter i sambandet mellan isvintrar, uppvärmning på våren och vattenstånd samt de olika faktorernas nämnda, ganska komplicerade inverkan på lek och yngelutveckling torde vara anledningen till, att något samband med de olika årsklassernas riklighet ej kunnat påvisas. Härvid får man också ha i minnet, att det är omöjligt att säkert veta, under vilket eller vilka år årsklasserna ifråga uppstått.

Som exempel på hur olika dessa klimatiska faktorer ha varit under perioder, då goda årsklasser av gädda likväl måste ha uppstått, kan anföras följande. De mest givande årsklasserna med goda fångster åren 1944—46 har sannolikt tillkommit under något eller några av åren 1939—41 med i vart fall under två av dessa år sena vårar och låga vattenstånd. Också de relativt rika årsklasserna 1921—23 härstammar från år med delvis tämligen sena vårar, medan vattenstånden under två av dessa år varit höga. Och årsklasserna omkring 1909—10 med i många fall mycket höga fångster åren 1914—15 har tillkommit under tidiga vårar med tämligen höga och relativt jämna vattenstånd.

De förutnämnda olikheterna mellan fångstkurvornas förlopp i de viktigare länen beror säkerligen delvis på olikheter i fiskets utövande under olika perioder. Men samtidigt har troligen också olikheter i de klimatiska faktorernas förlopp utmed olika kustområden spelat in. Även om exempelvis vattenståndsvariationerna under samma tid förlöper någorlunda likartat vid olika delar av ostkusten (jmf. sid. 45) kan dock enligt BERGSTEN (1955) under några dagars stormar betydande skillnader uppstå i vattenståndet vid olika platser.

Även olikheter i isförhållandena vid olika platser har säkerligen inverkat. De ovan berörda fångstsiffrorna från Åland, som helt avviker från dem på svenska sidan, kan möjligen tillskrivas skillnader i isförhållandena inom de åländska vattnen och sydöstra Finlands kustområden å ena sidan samt kustområdena vid Stockholms län å andra sidan. Att här föreligger vissa olikheter framgår av redogörelser av JURVA (1937) och RODHE (1955).

Slutligen bör måhända nämnas det samband som kunnat spåras mellan de bekanta solfläckperioderna om ca 11 år och vissa meteorologiska och biologiska förhållanden på jorden. Med god vilja kan man möjligen också i gädd- och abborrfångstens fluktuationer skönja en viss periodicitet med intervaller om ca 11 år.

Tabell 8. Utplantering av gäddyngel och ibland större gäddungar (i 1.000). — *Output of pike fry and fingerlings.*

	Län *Province*				
År	Stockholms	Södermanl.	Östergötl.	Kalmar norra	Kalmar södra
1930			500		
1			700		
2			530		
3			900		
4			700		
1935			1.000		
6			700		
7			760		
8			1.000	751	32
9			870	2.120	50
1940			1.000	1.900	—
1			1.000	500	—
2			1.000	1.545	550
3			1.000	840	—
4			2.200	1.110	—
1945			1.900	2.095	160
6			1.650	1.350	100
7	5.750	128	1.325	1.519	250
8	6.930	655	1.575	1.315	60
9	6.550	1.115	1.250	—	250
1950	8.100	1.115	1.900	780	550
1	7.680	436	2.000	615	720
2	6.300	3.483	1.800	375	100
3	3.150	2.120	1.100	—	—
4	4.100	2.260	2.000	—	—
1955	3.600	2.001	2.105	—	400
6	4.300	1.937	2.050	—	300

c. Odling och utplantering

I samband med det under förra halvseklet dominerande intresset för fiskodling igångsattes mångenstädes vid kusterna odling och utplantering av gädda. Abborren har däremot ej varit föremål för sådan odling i nämnvärd omfattning. Odlingen har huvudsakligen skett i hushållningssällskapens regi. I viss omfattning har dock gäddodling även bedrivits av enskilda fiskare och av fiskareorganisationer. Särskilt gäller detta Kalmar läns norra del. Tabell 8 visar antalet i de viktigare fångstlänen utplanterat gäddyngel. I allmänhet är det tämligen små mängder yngel som utsatts, högst 8 milj. år 1950 i Stockholms län. Vad angår resultaten av en dylik odling kan anföras följande. Rommängden hos en större gäddhona kan uppgå till 30—40.000 romkorn. SVÄRDSON (1945) har vid sina gäddlekstudier på basis av märkningar och kontroll av antalet lekande hongäddor beräknat den vid en strandsträcka av något över en halv km lagda rommängden till omkr. 14 miljoner, och i vart fall fastslagit att omkr. 1,5 milj. rom avlagts därstädes. Även om man enligt CARBINE (1943) och MONTÉN (1949) måste räkna med förluster på över 99 % mellan rom- och det något större yngelstadiet hos gäddan, ger dock en enkel räkneoperation vid handen att en utsättning av några miljoner yngel icke kan ha någon inverkan på beståndet inom större områden. Möjligen kan en begränsad utsättning av sådant större yngel, eller bättre månadsgamla ungar, därest miljön och förhållandena i övrigt under året är lämpliga, lokalt ge ett visst resultat. En del utsättningar, som skett inom ganska små och mera begränsade områden, uppges också i flera fall ha åstadkommit ökning i fångsterna på dessa platser, även om några säkra data häröver ej föreligger.

D. *De kortvariga fluktuationerna*

De ofta uppträdande kortvariga fluktuationerna i fångstmängden av gädda och abborre kan icke i första rummet bero på olika årsklassers växlande individrikedom. På grund av den flera år omspännande fångsttiden av en viss årsklass kan nämligen, därest årsklassens storlek vore avgörande, icke ett år med mycket god fångst följas av ett år med mycket dålig sådan, för att kanske nästa år åter ge ett gott utbyte. Dylikt kan endast inträffa med en fiskart, som huvudsakligen fångas under ett enda år, vilket ibland inträffar med siklöjan. Den olika fångståldern hos gädda och abborre talar också emot att sådana korta, men samtidiga fluktuationer kan bero på olika rika årsklasser. Däremot har säkerligen, som på sid. 35 och 43 framhållits, växlingar i fiskeintensiteten i viss mån bidragit till dessa kortvariga fluktuationer. Särskilt är det antagligt, att denna faktor medverkat till det större eller mindre utbytet under sådana år, då motsvarande fluktuationer förefunnits också beträffande andra viktiga fiskarter.

Emellertid har gädd- och abborrfångsten år för år varierat och även följt varandra på ett långt mera märkbart sätt än ifråga om andra arter och därjämte inte endast för vissa år utan för långa perioder. Beträffande fångsten av gädda och abborre är därför troligt, att även andra faktorer än fiskeintensiteten har inverkat, nämligen sådana som påverkar fiskets utövande eller som orsakar större eller mindre ansamling av fisken till lämpliga fångstområden. Utredningen rörande månadsfördelningen av årsfångsten av båda arterna har då visat, att huvudfångsten sker under första halvåret och speciellt under leken (b-perioden). Den har vidare visat att, även om själva lekfångstprocenten icke står i direkt korrelation till årsfångstens storlek, lekfångsten dock, absolut taget, varit större under de bättre än under de sämre åren, och att därjämte dessa växlingar varit mycket likartade i olika län. Med utgångspunkt härifrån kan man apriori antaga att väderleksförhållandena m.m. under lektiden bör vara avgörande för årsfångstens storlek, i den mån den ej beror på fiskeintensiteten eller beståndets storlek.

En tämligen tidig vår med därav följande lång fiskesäsong kan sålunda tänkas medföra god fångst. Likaså bör en längre period av varma, soliga dagar locka upp fisk på lekplatserna. Vidare bör i innerskärgårdarna ett relativt högt vattenstånd gynna utbytet, därigenom att lämpliga fiskeplatser då blir

Table 9. Goda, medelgoda och dåliga fångster och klimatiska faktorer. — *Big and poor catches and climatic factors.*

Fångst	År	Våren *Spring*	Medelvattenstånd[1] vid Landsort i *Mean water level in*		Stormar *Heavy winds*			Vattentillrinning *Water-supply*	Nederbörd[2] *Rainfall*		
			April	May	Apr.	May	June		Mars	April	May
God *Big*	1942	Rätt sen. *Late*	177	185	—	—	—	Dålig. *Poor*	29	56	190
	1945	Tidig. *Early*	213	200	+	—	+	God. *Ample*	32	102	—
	1946	Med. *Intermed.*	211	188	—	—	+	God	106	51	109
	1950	Tidig	204	187	+	+	—	God	44	112	108
Medelgod *Medium*	1941	Sen	176	178	—	+	—	Dålig	106	78	45
	1944	Med.	190	208	—	—	—	Med.—god	118	29	114
	1947	Med.	200	182	—	—	+	Dålig	138	50	32
	1949	Tidig	210	198	—	—	—	Dålig	55	110	92
	1951	Med.	196	180	—	—	—	God—med.	245	49	101
Dålig *Poor*	1940	Sen—med.	183	177	—	—	—	Dålig	194	43	74
	1943	Tidig	219	207	+	—	—	Med.	16	54	23
	1948	Med.—tidig	192	185	+	—	—	Med.	61	134	130
	1952	Med.	183	185	—	—	—	Med.—dålig	79	103	216
	1953	Med.	198	186	+	—	—	Med.—god	22	58	150
	1954	Rätt sen	179	173	+	—	—	Med.—dålig	164	60	122
	1955	Sen	187	205	+	—	+	Dålig	147	55	163

[1] Se figur 22.

[2] I °/₀ av medelnederbörden. — In percentage of the mean rainfall.

tillgängliga i större omfattning. Särskilt blir detta fallet, om vattenståndet är någorlunda likartat från april till maj, och om de dagliga variationerna under fisketiden ej är för stora. Slutligen bör också en god vattentillgång i på kusterna utmynnande vattendrag utöva en gynnsam inverkan på utbytet, genom att fisken lockas in mot strandområden, där den blir lättare att fånga. Nederbörden kan möjligen härvid ha en viss inverkan. Vindar och väderlek i övrigt spelar givetvis också en stor roll. Då emellertid speciellt vindens riktning och styrka måste verka ganska olika vid olika platser inom ett även så begränsat område som t.ex. ett län, har hänsyn ej tagits till denna faktor annat än beträffande uppträdandet av stormar under den viktiga lekfiskeperioden.

Det torde vara svårt att för hela kusten och även för samtliga berörda län, söka analysera dessa förhållanden. Då de största, kortvariga fluktuationerna förekommer i Kalmar läns södra del, och detta särskilt under 1940- och början av 1950-talen, under vilka år beståndet av både gädda och abborre måste varit rikt, och då vidare här fluktuationerna av båda arterna följer varandra år för år, har detta område tagits som exempel. I tabell 9 har då på basis av data från figur 23 över isvintrar, temperatur och vattenstånd under våren gjorts en mera allmän sammanställning rörande sen eller tidig vår m.m. Vidare har vattentillrinningen medtagits. Uppgifterna häröver är hämtade från i S.M.H.I:s årsböcker förekommande allmänna uttalanden. Från samma källa har slutligen införts tecken för om storm varit rådande

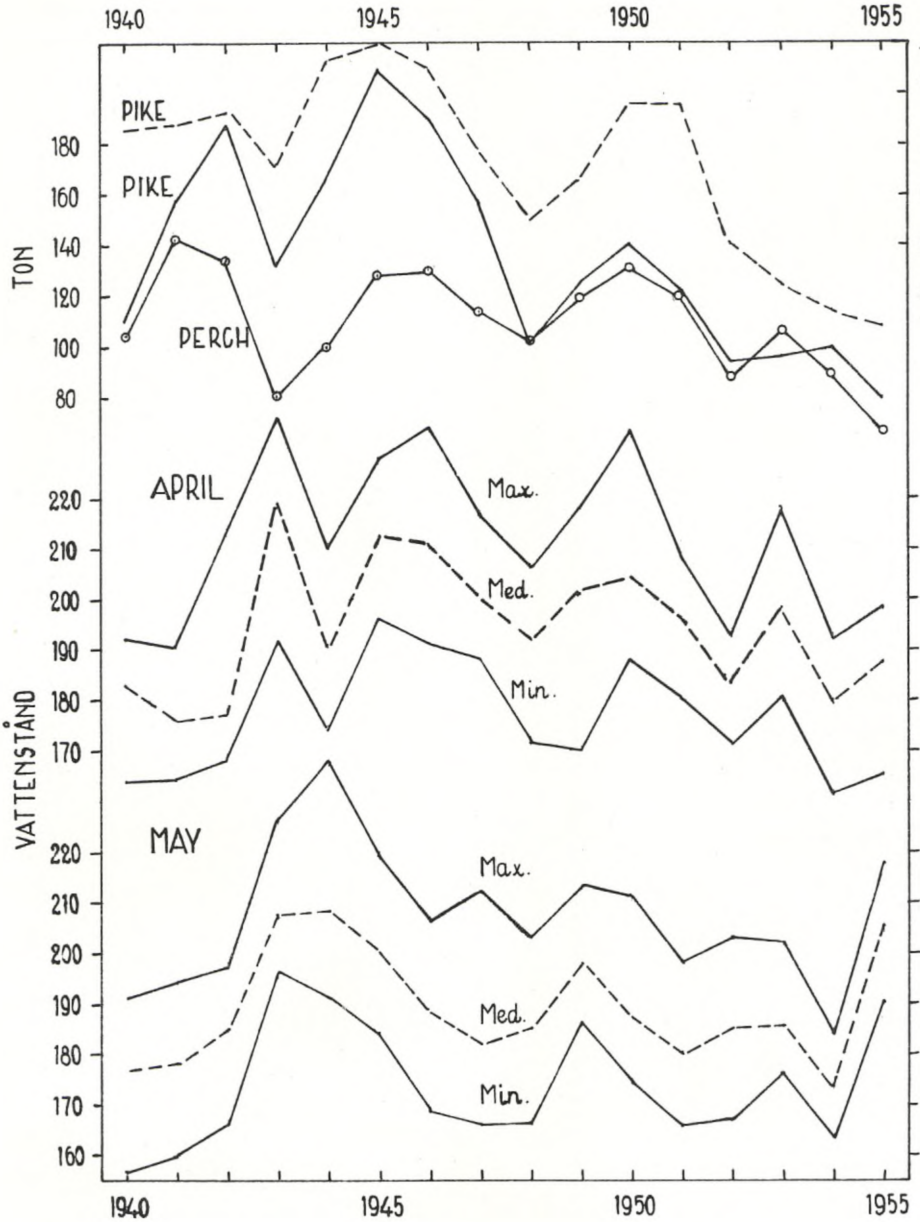

Fig. 24.

Medel-, maximi- och minimivattenstånd för april och maj månader under åren 1940—1955 samt årsfångsten av gädda och abborre.

Medium-, max.- and min.-waterlevel in April and May and the yield of pike and perch in the years 1940—1955.

i angränsande delar av Östersjön under månaderna april—juni. Också nederbördssiffror har beaktats. Som komplettering till denna tabell hänvisas till figurerna 22 och 23. För att ytterligare åskådliggöra vattenståndsvariationerna under vart och ett av de ifrågavarande åren har på figur 24 inlagts kurvor för medel-, maximi- och minimivattenstånd under de båda viktigaste fångstmånaderna. På samma figur återfinnes även fångstkurvor för gädda och abborre i Kalmar läns södra del samt för jämförelse, ehuru i annan skala, fångstkurvan för gädda för hela kusten. I den nyssnämnda tabellen har en uppdelning gjorts på tre grupper, goda, medelgoda och dåliga fångstår.

En granskning av tabellen visar följande. Både goda och dåliga fångster har förekommit under såväl tidiga som sena vårar. Sena vårar är möjligen vanligare bland de sämre fångståren. De goda fångståren 1945, 1946 och 1950 uppvisar förutom tämligen eller mycket tidiga vårar såväl god vattenföring som — 1945 och 1946 — höga vattenstånd. Det goda året 1942 med sen vår och ringa vattenföring har lågt, men från april till maj något stigande vattenstånd. Av de medelgoda fångståren uppvisar år 1941 likaledes en viss höjning av medelvattenståndet från april till maj. Trots sen vår och ringa vattenföring har fångsten blivit tämligen god. Detsamma gäller år 1949, där den ringa vattenföringen uppväges av tidig vår samt rätt högt och föga sjunkande medelvattenstånd. År 1944 med tidig vår och medelgod vattenföring uppvisar stigande vattenstånd. Bland de dåliga fångståren har 1940 och 1955 sen vår, låga — 1955 dock stigande — vattenstånd och ringa vattenföring. Sjunkande, men mycket högt vattenstånd utmärker år 1943, som i övrigt har tidig vår och medelgod vattenföring, men som trots detta gett dålig fångst. Av åren 1948, 1952 och 1953 med mera normalt inträdande vår har samtliga låga vattenstånd och frånsett 1952 även sjunkande. År 1954 slutligen kännetecknas av osedvanligt lågt vattenstånd hela våren.

Trots förekommande avvikelser tyder denna översikt på, att de tre faktorerna tidig vår, högt och jämnt eller från april till maj stigande vattenstånd, samt god vattenföring i tillrinnande vattendrag, såväl var för sig som ännu mera, om de uppträder samtidigt, medverkar till goda fångster av gädda och abborre. Sen vår, lågt och sjunkande vattenstånd samt ringa vattenföring bidrager däremot till sämre fångster av dessa fiskslag.

Förekomsten av stormar tycks inte visa något samband med de bättre eller sämre fångståren. Härmed är dock ej uteslutet att även svagare oväder kunnat inverka hindrande på fisket, speciellt kanske i ytterskärgårdarna. Någon inverkan av nederbördens större eller mindre riklighet har ej heller kunnat påvisas. Indirekt bör dock härigenom vattentillrinningen ha påverkats. Nederbörden har emellertid som synes varierat i hög grad under de olika vårmånaderna.

Förutsättningen för kortvariga fluktuationer, framkallade av nu diskuterade faktorer, är givetvis ett någorlunda rikt bestånd. De berörda kortvariga fluktuationerna har också främst inträffat under åren 1940—1950, då som tidigare antagits ett flertal rika årsklasser funnits. Under de mindre givande åren på 1920- och 1930-talen har detta slags fluktuationer varit relativt små.

VIII. Slutsatser angående behovet av skyddsåtgärder för gäddfisket

De ovan påvisade lång- och kortvariga fluktuationerna i gädd- och abborrfångsten vid Sveriges östersjökust har i det föregående ställts i samband med dels fiskeintensiteten och sådana faktorer som påverkar fiskets utövande, dels med växlingar i beståndens storlek på grund av årsklassernas olika individrikedom. Det har vidare på basis av tidigare undersökningar häröver framhållits att ett lekbestånds storlek, indirekt den lagda rommängden, i allmänhet icke har betydelse för dimensioneringen av en ny årsklass. Åtgärder för att hindra fångsten av gädda under leken i avsikt att få en rikare romläggning och ett därav följande bättre resultat av fortplantningen bör ur denna synpunkt vara tämligen värdelösa. Ett flertal sådana åtgärder har emellertid vidtagits i olika län.

Redan i början av detta århundrade påyrkades sådana åtgärder. I sina årsberättelser 1905 och 1907 till Stockholms läns hushållningssällskap nämner t.ex. fiskeriassistenten WAHLBERG att fjällfisket var mycket dåligt och syntes bli allt sämre med varje år. Den viktigaste orsaken härtill var »att söka i ett alltför ivrigt och oförståndigt fiskande under lektiden, då dessa arter (främst gädda och abborre) äro lättast att fånga, utan att samtidigt något göres för att underlätta fiskens fortplantning och trevnad». Och SCHAGER framhåller (1935) hurusom gäddfisket i Stockholms skärgård nedgått katastrofalt och att snarast åtgärder erfordrades för att speciellt minska det av tillfällighetsfiskare ofta som tjuvfiske bedrivna kastfisket. Han föreslog då införandet av fiskekort och igångsättandet av en synnerligen intensiv gäddodling.

En översikt av i gällande kustfiskestadgar nu förekommande föreskrifter till skydd för gäddans fortplantning är därför i detta sammanhang motiverad. I Stockholms län är sedan år 1939 fiske med vanliga gäddryssjor förbjudet under tiden 1—20 maj, och i Södermanlands län gäller alltsedan år 1936 ett liknande förbud under tiden 20 april—20 maj. Allt fiske med spinn, kast, angel m.m. är därjämte förbjudet i Stockholms län fr.o.m. 1 maj och i Södermanlands län fr.o.m. 20 april samt i båda länen till den 15 juni. I Östergötlands län är ända sedan år 1908 all fångst av gädda förbjuden under tiden 26 april—10 maj och därmed också alla för gäddfångst avsedda redskap. Vidare finnes under senare år förbud mot spinn- och angelfiske m.m., därest icke tillstånd härtill erhållits av länsstyrelsen. I Kalmar län är vanliga gäddryssjor ej förbjudna, men år 1932 infördes under tiden 1 april —15 maj förbud mot storryssjor, som då började komma i bruk i detta län.

Något förbud för gäddfångst finnes ej. I Gotlands län har sedan år 1920 fångst av gädda varit förbjuden i maj månad, och under tiden 16 april—31 maj får inte heller småryssjor brukas för fångst av fjällfisk. I Blekinge län saknas helt stadgebestämmelser rörande gädda. För fångst av abborre finnes endast undantagsvis några förbud.

En jämförelse med de förut anförda procenttalen för gäddfångsten under lektiden visar nu följande. För de tre områdena inom Kalmar län, där intet direkt gäddfiskeförbud föreligger, fångas under leken 30 resp. 29 % av årsfångsten inom Västervik- och Oskarshamn-områdena, men ända till 52 % inom Kalmar-området. Här har alltså rent lokala förhållanden och icke några olika förbudsbestämmelser orsakat skillnaden. I Blekinge län, där inga slags förbud finns, är lekfångstprocenten ca 32 %, medan i Stockholm- och Norrköping-områdena, trots här gällande förbudsbestämmelser tas mera, nämligen resp. 34 och 39 %. Och i Nyköping-området med liknande förbud utgör lekfångsten 29 %. De anförda siffrorna visar givetvis icke, att den begränsning av lekfisket, som avsetts med de olika förbudsbestämmelserna, varit helt utan verkan. Det är nämligen möjligt att lekfångstprocenten hade blivit större, därest intet förbud funnits. Men det är också möjligt att inom områden med förbud de fiskande mera intensivt ägnat sig åt fisket före och efter förbudstiden, än vad de annars hade gjort. I varje fall är det uppenbart att fångsten, trots förbuden, varit så intensiv, att den totala lekfångsten blivit av ungefär samma relativa storleksordning som inom de områden, där inga eller endast mera begränsade förbud rått, och där ett oavbrutet lekfiske kunnat bedrivas.

Därest förbuden medfört större romläggning och härigenom orsakat uppkomsten av rikare årsklasser, borde fångstkurvornas förlopp återspegla detta. Till en början kan då framhållas att, bortsett från Södermanlands län med dess för tidigare år tvivelaktiga statistik, samtliga län uppvisar stigande fångstkurvor för gädda, delvis även för abborre, från mitten av 1930-talet med kulmen åren 1945—1950, varefter fångstkurvorna åter går nedåt. Redan denna uniformitet talar för att fluktuationerna i fångstkurvornas förlopp icke kan tillskrivas de vid olika tidpunkt tillkomna och rätt skiftande förbuden. Säkert beror i stället denna överensstämmelse, som ovan framhållits, på faktorer som utmed stora delar av kusten orsakat uppkomsten av rikare eller fattigare årsklasser, eller som på liknande sätt påverkat fiskets utövande.

En närmare granskning av de olika länens fångstkurvor styrker ytterligare detta. Utan jämförelse med andra län kunde man exempelvis antaga, att den i stort sett jämna fångstökningen i Östergötlands och Gotlands län (fig. 6) berott på där sedan lång tid tillbaka rådande förbud. I Kalmar län (fig. 3 och 4) har emellertid avkastningen från mitten av 1930-talet ökat långt mera, än vad samtidigt varit fallet i de nyssnämnda länen, och även fångstkurvan för Blekinge län företer som nämnts under samma tid en visserligen svag men dock fortlöpande ökning. I Blekinge län råder ej något förbud, och i Kalmar län endast förbud mot storryssjor, som emellertid först på senare år blivit mera allmänna. Under början av 1900-talet utvisar därjämte Blekinge-kurvan en jämn ökning fram till 1915 för att sedan falla på samma sätt som i Östergötlands och Kalmar län. Fångstnedgången under 1950-talet är vidare starkt markerad såväl i Stockholms och Gotlands län, där förbud finnes, som i Kalmar och Blekinge län.

Särskilt påpekande förtjänar Stockholms län. Här sjunker gäddfångsten stadigt mot åren 1934—36, då den var lägst. Från och med år 1937 inträder, visserligen med smärre avvikelser, en fortlöpande ökning. I detta län fanns före år 1939 intet förbud mot ryssjefiske efter gädda. Därest genom det år 1939 inträdda ryssjeförbudet leken skulle ha underlättats och bättre årsklasser uppstått, kan detta tidigast ha påverkat fångsten under efteråret år 1942, medan fångstökningen börjat redan flera år tidigare.

Liknande förhållanden uppvisar också Kalmar län. Här tillkom visserligen förbudet år 1932, alltså några år före den början de ökningen av fångsterna. Men på grund av storryssjornas fåtalighet under åtskilliga år framåt kan en eventuell verkning av förbudet icke ha framträtt förrän in på 1940-talet, alltså åtskilliga år efter fångstökningens början. Och under de mycket kraftiga fångstökningarna från 1910 till 1914 och från 1922 till 1927 fanns intet förbud.

Ett bevis för att de långvariga fluktuationerna i gäddfångsten icke kunna tillskrivas ovannämnda förbudsbestämmelser har man också i det förhållandet, att fluktuationerna i abborrfångsten stämmer med dem hos gäddan. Även om detta delvis kan tillskrivas fiskets utövande (jmf. sid. 35), måste dock de mera långvariga fluktuationerna också hos abborren bero på förekomsten av olika rika årsklasser.

Vad här anförts ger därför icke stöd för antagandet att de gällande förbuden gagnat fortplantningen och ökat beståndet. Detta stämmer även med resultaten av vissa tidigare utredningar. Författaren till denna artikel har sålunda visat (ALM 1936), att avkastningen av gäddfisket i vissa fiskeribokföringssjöar hållit sig lika hög i sjöar, där huvudfångsten skett under leken, som i sjöar där fångsten mest förlagts till andra årstider. HESSLE (1934) framhåller i samband med diskussion av märkningarna av gädda i Östergötlands skärgård, att dessa i ett par försök givit återfångster på resp. 37 % och ända till 55 % och sålunda visat att fisket bedrives mycket intensivt. Till samma resultat kom TH. EKMAN (1915) med en återfångst under åren 1912—13 av 23 % märkta gäddor inom samma län. Trots detta intensiva fiske har fångsten i Östergötlands län genomgående ökat.

Som ett exempel på att ett intensivt gäddfiske är väl förenligt med en hög och icke sjunkande avkastning kan vidare anföras siffror från Börringesjön i Skåne. Enligt H. NORDQVIST (1942) och MONTÉN (1950) har där fisket under åren 1914—1948 alltmera intensifierats i avsikt att minska gädd- och abborrbestånden och få ett bättre utbyte av gös- och ålfisket. Resultatet har emellertid blivit att gäddfångsten ökat. Och denna fångst har i genomsnitt för hela perioden med ej mindre än 52 % av årsfångsten tagits under de båda lekmånaderna mars och april. Nämnas bör även att SVÄRDSON (1946) vid sina gäddlekstudier beräknat, att även vid ett mycket intensivt ryssjefiske på gäddans lekplatser endast omkr. 40 % av det lekande beståndet fångas. DAHR (1947) har också framhållit att den risk för s.k. överfiskning som teoretiskt finnes, därest stadgebestämmelser saknas, är synnerligen liten, och att det framförallt är andra faktorer som påverkar ett fiskbestånds individrikedom och fluktuationerna i fångsten av detsamma.

Som slutomdöme om dessa förbud för gäddfångst i samband med leken kan därför sägas, att de synas vara obehövliga, om med desamma avses att minska lekfisket för att därigenom öka fortplantningen och förbättra beståndet. En annan sak är att viss inskränkning i lekfångsten möjligen kan vara påkallad för att förebygga en alltför stor tillförsel av gädda till marknaden under en kort tid på våren med därav följande prissänkning för fiskarena.

Det skall givetvis heller inte förnekas, att ett mycket intensivt lekfiske inom ett begränsat område för något eller några år kan decimera beståndet. Rekrytering från angränsande områden kan emellertid då beräknas äga rum ganska snart.

Därest gäddbeståndet i något fall bör skyddas, måste en inskränkning av fisket före lektiden, särskilt det då ofta intensivt bedrivna angel- och saxfisket, anses viktigare än lekfiskeförbud. Vid detta fiske fångas ett stort antal gäddhonor, ofta kort tid innan rommen är mogen. Hela rommängden går då förlorad, medan däremot vid lekfisket ett flertal gäddor är i tillfälle avlägga en del av sin rom, innan de fångas. De tidigare anförda siffrorna för gäddfångsten under a-perioden, alltså månaderna januari—mars, och dess fördelning på dessa månader (fig. 7 och 8) visar också, att särskilt i februari fångsten i flera län och under vissa år kan vara högst betydande.

Mångenstädes talas nu om att det på senare år alltmera ökande sportfisket skulle inverka skadligt och i varje fall minska fångsterna för yrkes- och husbehovsfisket. Det är visserligen sant att praktiskt taget utmed hela den berörda kuststräckan avkastningen av både gädda och abborre nedgått under 1950-talet. Men motsvarande förhållanden ha varit för handen också under åren efter 1915 och efter 1927, under vilka perioder icke någon speciell ökning av sportfisket förekommit. Troligare är därför, att den senaste nedgången beror på samma faktorer, som framkallat tidigare fleråriga fluktuationer i beståndens storlek och i avkastningskurvorna, och att vi därför småningom åter bör kunna vänta ökande fångster.

IX. Sammanfattning

1. Fångsten av gädda och abborre utmed Sveriges östersjökust har i medeltal per år under tiden 1914—1955 uppgått till 629 resp. 440 ton. Den största fångsten kommer på Kalmar, Stockholms, Östergötlands och Blekinge län i nu nämnd ordning.

2. Fångstkurvorna för dessa fiskarter visar långvariga samt för de viktigare länen och för båda arterna i stort likartade fluktuationer med goda år omkring 1915, 1927, 1940—45 och 1950 samt dåliga år omkring 1920, 1930—35, 1948 och 1952—55.

3. Fångstkurvorna i de olika länen avviker dock i vissa avseenden från varandra och från kurvorna för hela kusten.

4. Förutom de långvariga fluktuationerna förekommer kortvariga, ofta årliga fluktuationer i fångstkurvorna, som också i flertalet fall är lika för de båda arterna och för de olika länen.

5. Mera än en tredjedel av årsfångsten av gädda och mera än hälften av årsfångsten av abborre tas under lektiden, medan endast 40 %, resp. 37 % tas under årets senare hälft.

6. Betydande variationer förekommer i lekfångstens procentuella andel av årsfångsten, och dessa variationer förlöper ofta likartat inom stora kustområden och även ibland för båda arterna.

7. Samstämmigheten i fluktuationernas förlopp för gädda och abborre beror främst på att huvudfångsten av båda arterna sker under en relativt kort tid på våren och med delvis samma redskap.

8. Både de lång- och kortvariga fluktuationerna sammanhänger i viss grad med fiskeintensiteten, särskilt under 1940-talet.

9. De långvariga fluktuationerna beror dock troligen mera på förekomsten av rikare eller fattigare bestånd, orsakade av mer eller mindre individrika årsklasser. En undersökning av de faktorer som kan tänkas orsaka årsklassernas dimensionering, särskilt temperatur och vattenstånd under rom- och yngelutvecklingen, samt tillgång på föda och fiender, har icke givit några positiva resultat. Detta sammhänger säkert med, att var och en av nämnda faktorer kan ha mycket olika inverkan i samband med förändring av andra påverkande faktorer.

10. De kortvariga fluktuationerna måste, utom på fiskeintensiteten, främst bero på faktorer, som inverkar på fiskets utövande och på fiskens ansamling på fiskeplatserna. Enär huvudfångsten sker under eller i samband med lektiden, blir det främst klimatiska faktorer under tiden april—juni som kommer ifråga. En sammanställning av dylika faktorer tyder på att tidig vår, högt och jämnt vattenstånd och god tillrinning i på kusterna utmynnande vattendrag medverkar till goda fångster. Sen vår, lågt, varierande vattenstånd samt dålig tillrinning orsakar sannolikt sämre fångster.

11. De flerstädes förekommande förbuden mot användning av viss slags redskap eller mot fångst av gädda under lektiden har säkerligen ingen bety-

delse, om därmed avses att gynna leken och upphjälpa beståndet. Lekfångstens storlek i förhållande till årsfångsten samt ökning eller minskning i fångsterna synes nämligen ha varit utan samband med gällande förbudsbestämmelser.

X. English summary

Introduction

In addition to certain salt-water fishes and to the anadromic species salmon and eel the brackish waters along the Swedish coast of the Baltic contain also several real fresh-water fishes. Some of these are of very great importance especially for the fishing in the archipelago. Most important are pike, perch, and whitefish. The latter is caught mainly in the more northern provinces, whereas the other two are fairly common along the whole extension of the coast. Also bream, roach, and ide are caught in rather great numbers. Fig. 1 shows the average yield in 5-year periods of the mentioned kinds of fish. In the following, however, only pike and perch will be dealt with.

Material

Information about the catch of these kinds of fish is found in the official statistical sources of Sweden since 1914, and in some cases even back to earlier times. These statistics comprise, however, only fishing carried on professionally or as an accessory means of obtaining a livelyhood which in Sweden is of a very great importance. The catches obtained by sport-fishing, which in later years have gained increasing importance, are unfortunately not included in these statistics.

These sources have now been examined with a view of studying the size of the catch and its fluctuations, and the underlying causes. In this connection it has been found desirable also to work out the seasonal variation of the catches, and an extensive material for the examination of these problems has been obtained from certain fish marketing associations along the eastern coast (Table 1).

The yield of the pike and perch fisheries in different years

The occurrence of pike as well as of perch is linked mainly to the larger archipelagos. These fish are rather stationary, and are caught mainly in fyke-nets, small traps and pound-nets as well as with gill-nets and by different methods of hook-fishing. The growth of the pike is much faster than that of the perch. Pike is caught in general when 3—7 years old, while perch is caught at the age of 5—10 years.

Fig. 2 shows the total annual catch of pike and perch along the Swedish coast of the Baltic. The average annual catch for the entire period amounts to 629 tons of pike and 440 tons of perch. The curves representing the catches of these types of fish in Fig. 2 show fluctuations of several years, which are on the whole parallel for pike and perch. Good years or good periods are found around 1915, 1927, 1940—45, and 1950, and bad times around 1920, 1930—35, 1948, and 1952—55. In addition to these fluctuations of longer duration the curves of the catches exhibit also yearly fluctuations, also these in most cases parallel for both kinds of fish.

Figs. 3—6 show the yearly catch, and Table 2 contains the size of the average catch, both absolute and as percentage of the entire yield of fishing in the Baltic, within the provinces, where fishing is of greater importance. This information shows the course of the curves of the catch to vary somewhat for the different provinces, but also that the good and the bad years coincide on the whole for several provinces. The fluctuations are greatest and in best agreement in the province of Kalmar (Figs. 3 A and 4) which is the most important for the two kinds of fish.

The pike and perch fisheries in differens months

Fig. 7 shows the catch during different months expressed in per cent of the annual catch, the figures being means for all the years for which information is available. In Figs. 8 and 9 the corresponding values for the different years are shown. Capture is seen to be concentrated mainly to the months of spawning, April–May for the pike, and April–June for the perch. There exist, however, great variations for different regions and also for different years. In Tables 3 and 4 the catch has been distributed over three periods: a) January–March, b) May–April for pike and May–June for perch, and c) the remaining months of the year. The great variations in the monthly catches set their stamp also upon these longer periods. This has the result that the differences between the maximum and minimum percentages for a certain region and for a certain period become fairly considerable. For the entire length of coast the catch during period b, i.e. the spawning time, reaches on the average for pike more than $^1/_3$ and for perch more than $^1/_2$ of the total annual catch. The later half of the year yields only 40 per cent and 37 per cent, respectively, of the annual catch.

The supply sent to the different marketing associations during different years has been calculated in per cent of the average supply. This applies also to the supplies during each of the periods a–c. The values obtained in this way have been entered into Tables 5 and 6 and into Figs. 10–15. This makes possible the following general statements. The fluctuations during different years in the supply to the associations receiving a large amount of pike and perch correspond in the case of pike on the whole to the fluctuations in the catch within the province in which the association is located (Fig.

10). We are thus entitled to assume that the established distribution of the catch during the three periods is typical for the Swedish fisheries for pike in the Baltic. The percentage of the catch during the spawning period (Fig. 11) is very variable, but has no connection with the size of the annual catch. Yearly fluctuations in the supply within each of the periods (Fig. 12) are as a rule similar for several regions of supply. This shows that along great stretches of the coast the size of the catch must have been influenced by the same factors.

In the case of the perch (Figs. 13–15) conditions are less clear than in that of the pike. Nevertheless, in some cases the same rules apply, and in certain instances agreement exists also between the two kinds of fish. Thus the annual catch was, for instance, good for both kinds in 1950 and 1951, and bad in 1953. Also the variations in the catch during the spawning time run fairly parallel for both kinds.

The reasons for the fluctuations in the pike and perch fisheries

Referring first to the close agreement between the fluctuations for the two kinds of fish, this must certainly depend upon the above-mentioned fact that in either case a great part of the annual catch is obtained during a relatively short time in spring. The places of capture and the fishing-gear employed are to a large extent the same. An intensive capture of one kind will then often entail also an intensive capture of the other as has been demonstrated for North-America lakes (HILE, LUNGER and BRUTTNER 1953, SMITH and KREFTING 1954). To this has to be added that the factors which can be thought to influence the strength of the year classes have in both cases similar effects. In spite of the different age at capture the years for the capture of simultaneously produced strong or feeble year classes coincide therefore at least in part. This result becomes still more noticeable if such extreme year classes are produced in the course of several consecutive years.

The intensity of fishing and the catch of different kind of fish

The fluctuations as well of longer as of shorter duration can partly be considered as due to the intensity of the fishing and to the development of the market prices. We are, unfortunately, without information about the time spent by the fishermen on the fishing. The statistics record only the number of the fishermen and of the gear used. Figs. 16 and 17 give information about the number of fishermen. This number shows a fairly uniform increase during the 1940's, followed by a decline. Also the number of fyke-nets and traps, which are the most important implement for the capture of pike and perch, increases (Fig. 18), but reaches its maximum already during the later part of the 1930's and the beginning of the 1940's. Since we have no information about the catch per unit of effort we have, however, no means of knowing to what extent the increased catch is connected with the increase in the intensity of fishing due to the increased number of fishermen and the greater number of fyke-nets and traps. The increased catch can, however, not be due to this increase only, since the yielding years around 1915 and 1927 did not show any corresponding increase in the number of the fishermen. To some extent an intensified fishing during the years of war 1915–1918 and 1940–1945 also may have caused the good catches in some of these years. But the top in the 1927-years cannot depend on this.

The Figs. 19 and 20 show the annual catch of the salt-water fishes, Baltic herring and cod, that are the most important within the provinces in question. Also these curves for the catch indicate a great increase during the 1940's. As far as the cod is concerned this rise continues also during the 1950's, whereas the catch of Baltic herring shows first a drop and then a renewed increase. These fluctuations depend, however, certainly upon simultaneous fluctuations in the size of the stock.

In order to examine if there is a closer connexion in the fluctuations in the yield of also other kind of fish, the fig. 21 gives the curves of the catch for the southern part of the province of Kalmar. From this it will be seen that in some years there seems to be a fair correlation in the curves. If this is not accidentally, it may depend on the fishermen, in some years fishing more frequently than in other years.

Table 7 shows the average price during the last 15 years. There seems to exist no connection between high prices and larger catches, or vice versa, during the different periods.

Year classes and stock of fish

It appears from the foregoing that the fluctuations of several years can hardly be caused only by the intensity of fishing or by factors connected with it. These fluctuations must, therefore, be linked up with fluctuations in the size of the stock which in its turn are caused by stronger or weaker year classes. The strength of the year classes can depend upon the spawning stock, climatic factors, and hatching.

Several investigations and experiments dealing with different kinds of fish have shown that, within certain limits, no closer connection exists between the number of spawning fish and the strength of the new year class. Also in the case in question nothing points to the existence of such a connection.

There exists no doubt that the climatic factors are the deciding ones. Among them the level of the water and its temperature and the wind-conditions during spring play probably the greatest rôle. An early and warm spring ought on the whole to favour the development of roe and fry, and also the production of a strong year class. The same applies to a fairly stable and not too low water-level by the spawning at shallow waters. For the pike spawning at greater depths the water level cannot of coarse have any influence. Stormy and bad wheather may hurt the tiny fry of pike and perch and throw them to the shores, where they will be killed. Several of these factors have been studied in greater detail since 1909, inclusive, i.e. 5 years before more extensive statistics were started. Fig. 22 shows that the level of the water along the coast varies considerably from year to year, from month to month, and even from day to day. Differences of 10–20 cm and sometimes still more are fairly common. With regard to temperature we remark that severe winters with much ice are most often followed by low temperatures during the months of spring, and thus by a late spring. Yet Fig. 23 shows that this has not always been the case. The climatic conditions have been altogether rather complicated. Neither has it been possible to establish any direct connection between the production of strong year classes and certain conditions of the water-level or of the temperature nor of the wind. Thus such year classes must have been produced during years which in respect to these factors have been rather dissimilar. The most yielding year classes with rich catches in the years 1944–46 have been produced during the years 1939–41 with, at all events during two years, late springs and low water-level. Also the relatively strong year classes 1921–23 are derived from, in part, rather late springs, whereas the water-level has been high during two of these years. And the year classes 1909–10, with in many cases very rich catches in the years 1914–15, have been produced during early springs with fairly high and relatively stable water-level.

Table 8 contains the number of fry of pike planted out in the provinces which are more important from the point of view of fishing. It is obviously impossible that these relatively small quantities of fry could have influenced the strength of the stock over larger areas. Neither do we have any certain proof that the stock and the cath of pike should have increased locally in the places, where larger plantations have been carried out, even if the fishermen in several places believe this to have been the case. Hatching of perch has not taken place on an appreciable scale.

The yearly fluctuations

Such fluctuations of short duration can of course not depend upon fluctuations in the strength of the year classes. This is made impossible by the circumstance that the age of capture comprises several years, and is somewhat different for the two kinds of fish. We must instead be faced here with factors which have had either a favourable or an unfavourable influence upon the practising of the fishing during several years, or which have caused the fish to collect in larger or smaller numbers in the spots which are most suitable for fishing. With a view of examining this question there have been collected in Table 9 informations about late or early spring, water-level, the flow of water in the watercourses leading to the coast and the wind-conditions, all this for the months April–June, these being the most important for fishing. Also in Fig. 24 some of these factors have been demonstrated. Though it has not been possible to establish any tangible correlation between the amount of fish caught and the factors mentioned, it is nevertheless obvious that good years most often are characterized by a relatively high and stable water-level, a good supply of water, and an early spring. We can therefore suppose that these factors have had a positive influence upon the size of the catch.

Conclusions regarding regulation of the pike and perch fisheries

In certain of the mentioned provinces the provincial authorities have issued regulations forbidding the capture of pike or the use of fyke-nets or traps during a certain part of spring. No such prohibitions exist on the other hand for perch. The increase or decline of the pike fisheries in the different provinces does, however, not exhibit any connection with the existence or non-existence of regulations of this kind. Also the size of the catch of spawning fish expressed in per cent of the annual catch is independent of it. In the province of Kalmar, for instance, the catch during the period b (spawning period) was 29 per cent and 30 per cent within two regions, whereas it amounted to 52 per cent of the annual catch in a third region.

Such regulations are certainly superfluous, if they are intended to reduce the fishing during the spawning time with a view towards increase of propagation and amelioration of the stock. A certain restriction of fishing during the spawning time might, however, be called for in order to prevent an excessive supply of the market with pike during a short time in spring with the consequent drop in price obtained by the fishermen. If it is necessary to protect the stock of fish by regulations forbidding of hook fishing in the months before the spawning time could be recommended. As will be seen from the figures 7 and 8 rather much pike will be caught in some years in these months.

XI. Litteratur

ALM, G. 1926. Notizen über Uferwassertemperaturen der Seen im Frühling. *Archiv f. Hydrob. XVII: 501—506.*

— 1936. Huvuddragen av fiskeribokföringsverksamheten. *Meddel. Undersökn. försöksanst. sötvf. 11: 1—64.*

— 1938. Gäddfisket vid våra kuster. *Sportfiskaren. 5: 1—4.*

— 1949. Ökar eller minskar gäddan och abborren vid våra kuster? *Ibidem 1: 1—3.*

— 1952. Year Class Fluctuations and Span of Life of Perch. *Inst. Freshw. Research. Rep. 33: 17—38.*

BERGSTEN, F. 1925. Vattenstånden vid Rikets kuster år 1887—1921. *Stat. Met. Hydrogr. Anstalt. Meddel. II: 1—85.*

— 1950. Vattenståndens varaktighet utmed svenska kusten. *Geogr. Annaler. 32: 165—178.*

— 1955. Winds and Water levels on the coast of Sweden. *Ibidem. 37, 3/4: 119—140.*

CARBINE, W. 1943. Egg Production of the northern Pike. *Ann. Arbor. Mich. Acad. Science and Arts. Papers. 29: 123—137.*

DAHR, E. 1947. Om överfiskningsproblemet i insjöar och skärgårdsvatten. *Sv. Fisk. Tidskr. 7: 130—136.*

— 1949. Biologiska betraktelser över nyttan av fiskinplanteringar i naturliga sjöar och vattendrag. *Ibidem 12: 171—175.*

EKMAN, TH. 1907. Gäddans lekplatser i skärgårdar. *Sv. Fisk. Tidskr. 3: 88—89.*

— 1915. Meddelanden rörande utförda märkningar av gädda m.fl. fiskar i Södermanlands och Östergötlands skärgårdar. *Ibidem 2: 62—68.*

FISKERISTYRELSENS fyrskeppsundersökning. *Åren 1948—49, 1950.*

GOTTBERG, G. 1917. Om gäddans tillväxt i Ålands skärgård. *Finlands fiskerier. 4: 223—243.*

— 1923. Gäddmärkningar i Ålands skärgård. *Fiskeritidskr. f. Finland. 1: 1—6.*

HAGMAN, N. 1946. Gäddfångsternas årliga växlingar i skärgårdshaven. *Sv. Fisk. Tidskr. 1: 15—21.*

HALME, E. 1952. On the influence of climatic variations on fish and fishery. *Soc. Geogr. Fenn. 75: 89—96.*

HESSLE, CHR. 1934. Märkningsförsök med gädda i Östergötlands skärgård åren 1928 och 1930. *Meddel. Unders. försöksanst. sötvf. 3: 1—17.*

HILE, R. and JOBES, W. 1941. Age, growth and production of yellow perch of Saginaw Bay. *Trans. Amer. Fish. Soc. 70: 102—122.*

— LUNGER, G. F. and BUETTNER, H. J. 1953. Fluctuations in the fisheries of State of Michigan waters of Green Bay. *Fish and Wildlife Service. Fishery Bulletin. 75: 1—34.*

HYDROGRAPHICAL OBSERVATIONS ON SWEDISH LIGHTSHIPS 1952—1956. *Fishery Board of Sweden Ser. Hydr. Rep. 1, 3, 4, 6.*

JURVA, R. 1937. Atlas der Eisverhältnisse des Baltischen Meeres an den Küsten Finnlands. *Helsinki Institute of Marine Research.*

— 1952. On the variations and changes of freezing in the Baltic during the last 120 years. *Soc. Geogr. Fenn. 75: 17—24.*

JÄRVI, T. H. 1942. Die Bestände der Kleinen Maränen und ihre Schwankungen. *Acta Zoolog. Fennica. 32: 1—89.*

KOCZY, F. F. 1954. Medelvärden av temperatur och salthalt vid svenska fyrskepp 1923—1952. *Fishery Board of Sweden. Ser. Hydr. Rep. 5: 1—59.*

LIEDES, M. 1955. Fiskfångsten och dess värde under år 1953. *Lantbruksstyrelsen Helsingfors. Skrifter 1955: 1—3.*

LILJEQUIST, G. H. 1943. The severity of the winters at Stockholm 1757—1942. *Stat. Met. Hydrogr. Anst. Meddel. 46: 1—24.*

— 1950. On the fluctuations of the summer mean temperature in Sweden. *Sver. Met. Hydrol. Inst. Meddel. Ser. B (7): 1—24.*

METEOROLOGISKA IAKTTAGELSER I SVERIGE. 1910—1918. *K. V. A. Meteorol. Centralanst. Bd 52—60.*

MONTÉN, E. 1948. Undersökningar över gäddynglets biologi och några därmed sammanhängande problem. *Skr. Södra Sver. Fiskeriför. 1: 3—38.*

— 1949. Studier över yngelförlusternas orsaker i fria vatten och i dammar II. *Ibidem 2: 20—101.*

— 1950. Ett praktiskt fiske- och fiskevårdsförsök i Börringesjön i Skåne. *Ibidem. 1: 19—53.*

NILSSON, D. 1921. Några insjöfiskars ålder och tillväxt i Bottniska viken och Mälaren. *Meddel. Kgl. Lbrstn. 231 (2): 1—56.*

NORDQVIST, H. 1942. Fisket i Börringeområdets sjöar t.o.m. år 1940. *Skr. Södra Sver. Fiskeriför. 2: 32—55.*

RODHE, B. 1955. A Study of the correlation between the ice extent, the course of air temperature and the sea surface temperature in the Åland archipelago. *Geogr. Annaler 37, 3/4: 141—163.*

ROLLEFSEN, G. 1949. Fluctuations in two of the most important Stocks of Fish in Northern Waters, the Cod and the Herring. *Rapp. Proc. Verb. Cons. Perm. Int. Exp. Mer CXXV. 3: 33—35.*

ROSÉN, N. 1920. Om Norrbottens saltsjöområdes fiskar och fiske. *Meddel. Kgl. Lbrstn. 225 (6): 1—94.*

SCHAGER, C. H. 1935. Fiskekort i Stockholms skärgård. *Sv. Fisk. Tidskr. 12: 318—320.*

SEGERSTRÅLE, C. 1932. Über die jährlichen Zuwachszonen der Schuppen und Beziehungen zwischen Sommertemperatur und Zuwachs bei Abramis brama. *Acta Zool. Fennica. 13: 1—42.*

— 1947. Rön och erfarenheter av gäddodlingsarbetet. Fiskodlingens Vänner. Helsingfors.

— 1948. Gäddan och abborren i sydfinländska kustvatten. *Skärgårdsboken, Utg. av Nordenskiöld-Samfundet, Helsingfors. 401—441.*

SMITH, JR. L. L. and KREFTING, L. W. 1954. Fluctuations in production and abundance of commercial species in the Red Lakes, Minnesota, with special reference to changes in the Walley population. *Trans. Amer. Fish. Soc. 83: 131—160.*

SVENSKA HYDROGR.-BIOL. Kommiss. *Fyrskeppsundersökn. Åren 1923—1947.*

SVERIGES METEOR. HYDROL. Institut. *Årsböcker 1919—1955.*

SVERIGES OFFICIELLA statistik. Fiske. *Statist. Centralbyrån 1914—1955.*

SVÄRDSON, G. 1945. En gäddlek i siffror. *Sv. Fisk. Tidskr. 9: 187—192.*

— 1946. Gäddlekstudier. *Skr. Södra Sver. Fiskeriför. 2: 34—59.*

TIDEMAN, M. 1920. Kan ett intensivt lekfiske inverka menligt på gäddfisket. *Sv. Fisk. Tidskr. 3: 85—88.*

TÄGTSTRÖM, B. 1946. Några reflexioner över gäddfiskets växlingar. *Sv. Fisk. Tidskr. 5: 105—107.*

WESENBERG-LUND. 1912. Über einige eigentümliche Temperaturverhältnisse in der Litoralregion der Baltischen Seen. *Intern. Rev. Hydrogr. Hydrob. V: 287—306.*

ÅNGSTRÖM, A. 1946. Sveriges klimat. *Stockholm. 1—105.*

ÖSTMAN, C. J. 1939. Om sambandet mellan isläggningen vid svenska ostkusten och meteorologiska faktorer. *Stat. Met.-Hydrogr. Anst. Medd. 7 (5): 1—16.*

A Study of the Whitefish (*Coregonus*) of the Sundsvall Bay District[1]

By Arne Lindroth

Contents

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[1] Report from The Swedish Migratory Fish Committee.

Introduction

Catches of whitefish from the rivers and from the coastal areas play an important role for the fisheries of the Sundsvall district in the north of Sweden. In the rivers Indalsälven and Ljungan the whitefish is taken in seines during late summer and autumn, when the fish migrate from the sea to spawning grounds in the river. On the coast it is caught in bag nets of differing designs ("storryssjor" or "kittor") or gill nets during a great part of the year (May to November).

The hydroelectric schemes encroaching upon the rivers to a greater and greater extent affect the river fish populations adversely, and among them the whitefish. This fact has made basic information on this fish necessary and some results of investigations carried out 1951—1956 are here presented. (As the material has not yet been subject to scale-reading problems connected with age, growth and exploitation are not considered in this paper.)

I. Species of whitefish in the area

From early times it has been known that whitefish populations from the coastal area undertake regular spawning migrations up the great rivers Indalsälven and Ljungan. There exist however spawning grounds also in the brackish water round the coast although these have been known only locally to the fishermen. The question of the taxonomie position of the different populations naturally arises.

a. *Material and methods*

Samples of whitefish were obtained from the commercial fishery, and as a rule taken in seine nets in the rivers and bag nets, only in very few instances in gill nets, on the coast. The fish were examined as regards sex, stomach content, number of gillrakers on the first left arch and in some cases the number of scales in the lateral line was counted.

Accidental catches of whitefish, mostly young fish from Indalsälven, were obtained with seine nets, dip nets and a smolt trap in the mouth of the river.

In one rearing experiment whitefish ova from known parents of two different populations were fertilized and hatched in the state hatchery of the district. The hatched fry was reared in large, drainable ponds from which, in the autumn, samples were taken of the one summer old young.

b. *Results*

1. Gillrakers in the different populations

The results of the examination of 26 samples of whitefish are summarized in Fig. 1 and Table 1. The samples may be divided into four groups

I Samples of river spawning or river migrating populations from Indalsälven, Ljungan and Ljusnan (for their situation see Fig. 4)
II Samples of coast spawning populations taken at spawning time
III Samples from the coast taken out of spawning time
IV Accidental catches

Only those samples from groups I and II and partly from IV can be regarded from a genetical point of view as representing fairly homogenous populations.

The mean numbers of gillrakers for the various river spawning populations in group I vary between 30.2 and 32.2. Corresponding figures for the coast spawners are 27.0 to 28.4.[2]

The coast samples from Lörudden (30.1 to 31.0) can naturally be classed with those from the river populations and may well consist mainly of fishes from river spawning populations.

According to the gillraker countings the Sundsvall bay district seems to house two forms of whitefish, one river spawning and one coast spawning form. As shown by the accidental catches individuals or shoals of other populations can sometimes be met with in the river (this question will be discussed at some length in a following chapter).

2. Gillrakers at different sizes

Gillraker countings on first summer whitefish young mostly taken in the smolt trap in the mouth of the river Indalsälven are shown in Fig. 2. The gillrakers begin to be visible as small knots on the gill arch at a fish length of about 20 mm. At a length of say 8 to 10 cm total length (that is at the end of their first summer) the young have about 30 gillrakers which is — or cannot be far from — the definitive number.

3. Genetical nature of the two main forms

The above finding entitles us to use the gillraker countings in the one summer old young in a rearing experiment, as characterizing the daughter generation and, accordingly, as a test of the genetical nature of the two whitefish forms. In this experiment the different hatches from the river and

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[2] It is to be noted that the highest number, 28.4, is found at a locality close to the mouth of river Indalsälven.

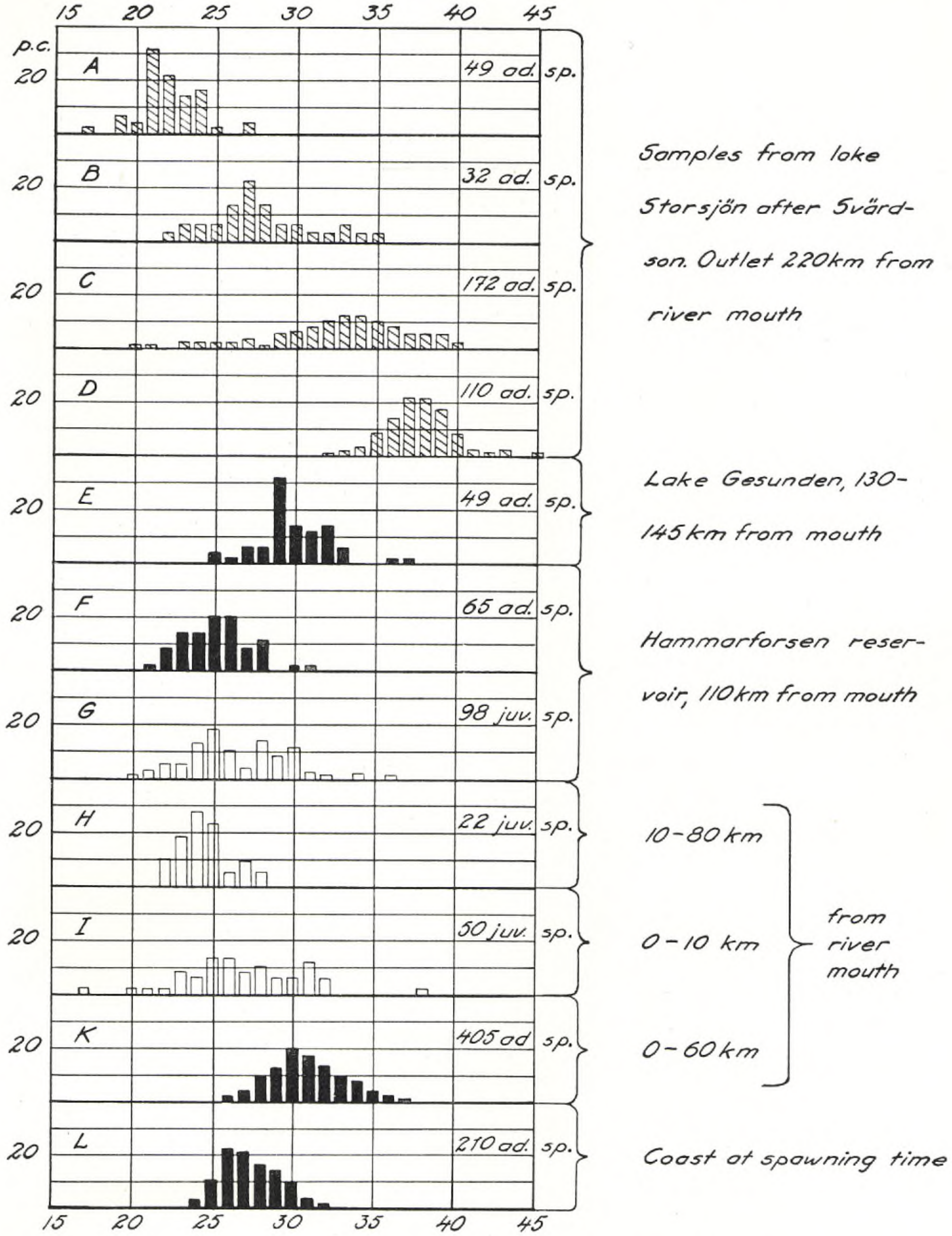

Fig. 1. Percentage distribution in gillraker classes of whitefish from Indalsälven river system and the coast.

Black piles: populations in spawning (or spawning migration—K)
Grey piles: adult fish (A—D SVÄRDSON 1953)
White piles: juvenile fish.
K: *Coregonus lavaretus,* the river spawner
L: *C. nasus,* the coast spawner.

Table 1. Samples

Samples			Sex ♂ : ♀	Gill									
Origin	Date	Nr.		Mean nr.	Percentage distributio								
					17	18	19	20	21	22	23	24	2
I. Rivers accessible from the sea													
A. Indalsälven													
1. Bogrundsvarpet	1951 20/9	100	62:38	30.7									
2. Sillre	1951 26/9	36	56:44	30.9									
3. Bogrundsvarpet	1951 8/11	50	14:86	31.3									
4. Östloning	1951 16/11	20	—	31.8									
5. Bogrundsvarpet	1952 20/9	50	78:22	30.2									
6. Tomming	1952 14/11	50	—	32.2									
7. Bogrundsvarpet	1953 29/9	49	69:31	31.1									
8. Liden	1953 25/11	50	28:72	31.1									
B. Ljungan													
9. Below dams	1951 24/9	60	73:57	30.9									
10. ,, ,,	1952 4/9	50	60:40	31.0									
C. Ljusnan													
11. Below dams	1952 28/10	50	32:68	31.3								2	
Total and mean		565		31.04									
II. Coast at spawning time													
12. Åvike	1951 31/10—6/11	50	52:48	27.7								4	1
13. Bergafjärden	1951 7/11	50	74:26	27.5								4	
14. Stornäset (Alnö)	1951 24/11	10	90:10	28.4								10	
15. Bergafjärden	1953 21/10	50	54:46	27.5								2	1
16. Slädaviken (Alnö)	1953 4/11	50	22:78	27.0								2	1
Total and mean		210		27.48								3	1
III. Coast out of spawning time													
17. Lörudden	1951 10/9	100	51:49	30.1									
18. ,,	1952 11/7	45	51:49	30.8									
19. ,,	1952 3/9	50	40:60	31.0									
20. Slädaviken	1952 22/9	50	36:64	28.7									
IV. Various samples													
A. Indalsälven water system													
21. Lake Gesunden	1951 15/11	6	100:0	25.3							33		3
22. ,, ,,	1951 15/11	49	98:2	29.7			2						
23. Hammarforsen reservoir	1956 14/9—13/10	65	34:66	25.1					2	8	14	14	2
24. ,, ,,	1956 1/10—10/10	98	—	26.5				1	3	5	5	13	1
25. 0—80 km from mouth, table 6	1951—1956	72	—	26.2	1			1	1	6	12	13	1
B. River Ljusnan													
26. Above lowest dam	1951 2/8	5	—	37.4									
Total		1,315											

coast forms were incubated and reared, until their first autumn under practically identical conditions: owing to the optimum conditions in the large rearing ponds, they attained a length of 17 to 19 cm (means).

The result of the rearing experiment is shown in Table 2. Offspring from coast spawners, the male giving 28 and both females 26 gillrakers, show means of 27.1 and 27.9 respectively. Brood from river spawners of whitefish.

akers															Scales in lateral line Mean nr.	Comments
n classes																
26	27	28	29	30	31	32	33	34	35	36	37	38	39	40		
	5	8	14	26	13	12	13	7	1	1						
		14	16	16	11	14	6	11	3	3	3					
2		8	14	8	24	16	14	8	2	4						
	5		5	25	15	20	10		5	15						Selected females only
8	4	8	14	20	20	8	8	4	2		2					
		4	8	12	16	14	20	10	8	4	4				94.9	
2	10	12	15	15	24	8	6	0	8						93.7	
4	2	6	14	12	18	16	6	18	2	2					96.74	
2	3	2	23	12	20	15	10	10	3							
	4	8	10	20	16	18	8	14	2							
2	4	2	10	14	24	14	6	12	4	4	2				96.5	
2	4	7	14	17	18	14	10	8	3	2	1					
18	20	6	16	22	4											
16	28	20	16	4	4	2										
10	30	10	10		10	10	10									
16	14	26	18	6	2	2									91.38	
36	20	14	10	2	2	4									92.0	
21	21	16	15	8	3	2	1									
4	8	14	14	16	16	11	9	7								
2	7	9	4	20	23	16	9	4	2	4						
4	2	6	18	4	30	8	14	6	6	2						
10	6	28	16	24	8	2	2									
	17		17													Length 35—40 cm
2	6	6	31	14	11	14	6			2	2					"Smärling", length about 20 cm
20	8	11		2	2											Adult fish
10	4	14	8	11	2	1		2		1						Juvenile fish
12	8	8	4	4	8	4						1				Juvenile fish
									40			20	20	20		Juvenile fish

have 32.7 and 33.2 gillrakers (mean figures) the male having 34 and the females 30 and 31.

The rearing experiment has therefore proved that the difference in number of gillrakers between the two main forms of whitefish in the Sundsvall bay district is genetically fixed and that the forms are genetically different. According to SVÄRDSON (1957 and personal communication) the forms are to

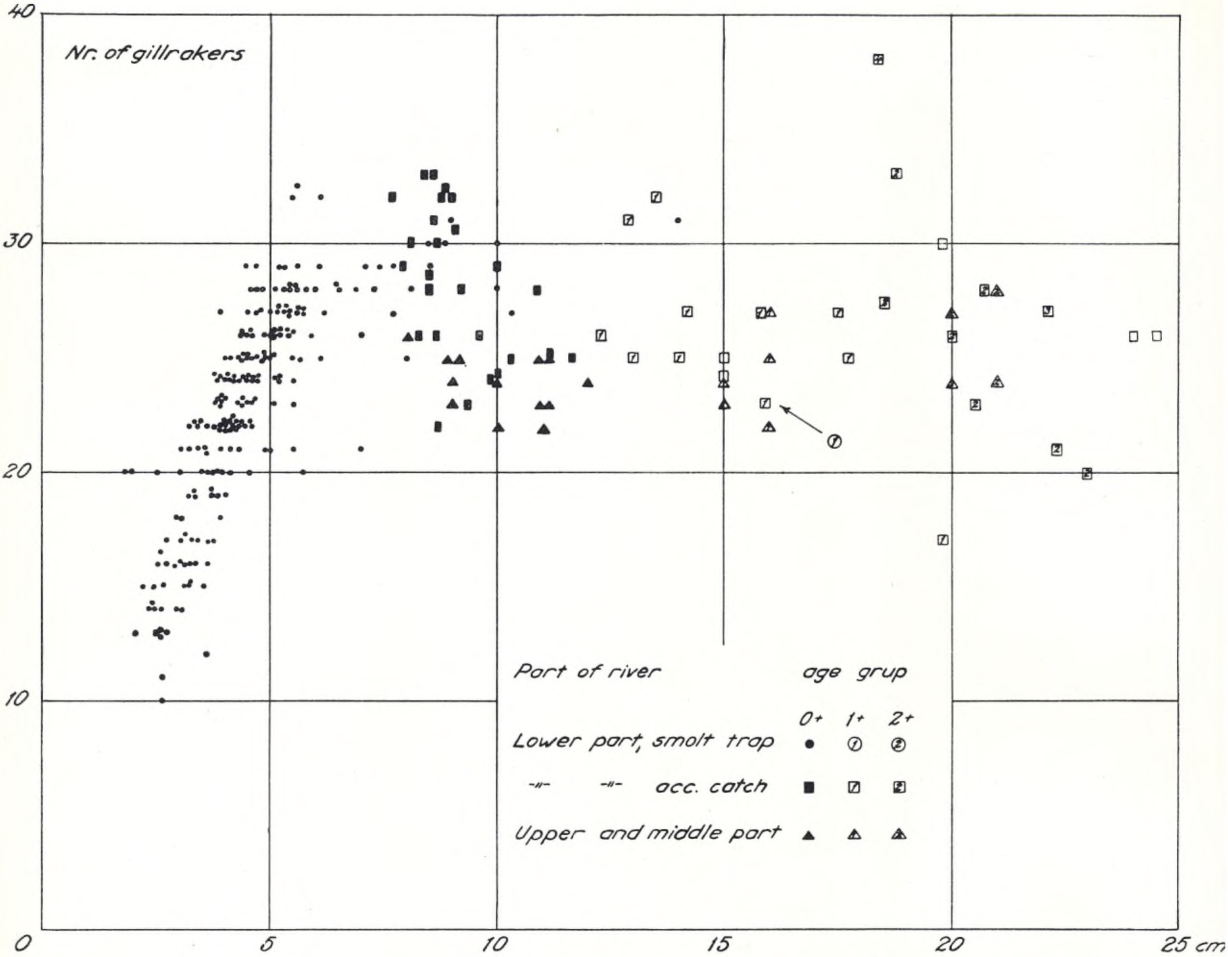

Fig. 2. Gillrakers plotted against total length in juvenile whitefish from smolt trap 1952—1955, and accidental catches.

be regarded as separate species: *Coregonus lavaretus* L., the river spawning species, and *C. nasus* PALLAS, the coast spawning species.

4. Taxonomical result of tagging experiments

It may be mentioned here that the tagging experiments reported in the following chapter have comprised 179 specimens of *C. nasus* 712 of *C. lavaretus* and 401 from mixed or unspecified populations. Of the 179 coast specimens 73 have been reported as recaptured, but only one from the rivers, whereas the riverspawning *C. lavaretus* is reported at spawning time almost exclusively from the home river. There seems then to exist a biological sexual barrier between the two species of the district.

Table 2. Rearing whitefish from two different populations 1952—1953.

Expt nr[1]	1	2	3	4
Origin of parents	Coast	Coast	River	River
Fertilization	Oct. 22	Oct. 22	Nov. 13	Nov. 13
Liberation in pond	Apr. 28	Apr. 28	May 2	May 5
Fishing of pond	Sept.	Sept.	Sept.	Sept.
Nr. of young examined	50	50	50	50
Lengts, cm male	34	34	39	39
female	34	34	42	37
young, mean	18.4	19.4	17.3	17.2
Scales in lateral line male	94	94	102	102
female	95	94	89	95
young, mean	97.1	95.4	98.2	96.2
Gillrakers male	28	28	34	34
female	26	26	30	31
young, mean	27.1	27.9	32.7	33.2
Distribution in gillraker classes 24	5	2		
25	—	4		
26	9	2		
27	15	8		
28	14	17		
29	6	11		
30	1	4	1	
31		2	9	5
32			15	10
33			12	13
34			8	15
35			1	4
36			3	3

[1] One more experiment was made giving a twotipped frequency curve for the gillrakers and a diverging mean in the offspring. It is thought that some mixing of different batches of fry must have occurred.

c. *Discussion*

For several years a large portion of the work of the Institute of Freshwater Research in Sweden has been devoted to the speciation problems of the genus *Coregonus*. For general discussions of these problems the reader is therefore referred to the papers by SVÄRDSON (1949 etc.). The results arrived at by the present author do not contribute anything that is in principle new to the general discussion of whitefish taxonomy. A few points may, however, be mentioned.

The usefulness of the number of gillrakers as a taxonomic characteristic has been vindicated already by NÜSSLIN and THIENEMANN and by SVÄRDSON in his later papers (1950 etc.) as well as by several other authors. It is corroborated by the material added through this investigation. This applies especially to the rearing experiment.[3] Offspring of known parents of two

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[3] Note the values for scales in lateral line, Table 1 and 2. Without discussing the genetical nature of this feature it is clear that it had offered no opportunity of characterizing the populations treated in this investigaion.

species, reared under almost indentical external conditions, remained unaltered as to the number of gillrakers, thus confirming earlier rearing experiments (SVÄRDSON 1952).

In the case of the coast spawning *C. nasus*, the rearing involved a transplantation from brackish water (a few per mille of salt content) to fresh water. SVÄRDSON is certainly right when he, in opposition to his former view (SVÄRDSON 1951), states that "water quality cannot, thus, be said to modify the gillraker apparatus" (SVÄRDSON 1952).

JÄRVI (1940) shows that whitefish young in their first autumn have the definitive number of gillrakers and SVÄRDSON (1950, 1952) communicates values indicating that this is attained at a length of between 7 and 10—12 cm. The material presented here (Fig. 2, showing the increase in number of gillrakers as the length of the fish increases) corroborates these statements, and shows that in *C. lavaretus* in Indalsälven the definitive number is attained at a size of about 8—10 cm.

For the systematic position of the two main whitefish species of the Sundsvall bay district, *C. lavaretus* and *C. nasus,* and for their geographical distribution the reader is referred to future reports by SVÄRDSON from the Institute of Freshwater Research.

II. Movements

a. *Methods*

The movements of the Sundsvall bay and adjoining populations of whitefish have been studied by means of taggings. The tag used is a cellulloid plated piece of cardboard with stainless steel wire of a type introduced by the Migratory Fish Committee in Sweden (see CARLIN 1955; reproduction in LINDROTH 1952). The tag measures 20×4 mm and is attached to the fish just beneath the hind margin of the dorsal fin. The length of the fish is recorded, sometimes also the weight, before liberation.

The fish for tagging are obtained from seines in the river or from bag nets at the coast and invariably liberated at or close to the place of capture. It may be observed that whereas a seine haul is thought to catch individuals of one or a few shoals during its short period of operation a bag net gathers fish passing during one or several days. The homogenity of the catch in the former type of gear must be far greater.

Following DAHR (1947) I am aware of the fact that the vitality of the fish may be influenced by the tagging and that this objection is valid mainly with regard to calculations concerning survival and exploitation without upsetting studies of migratory movements.

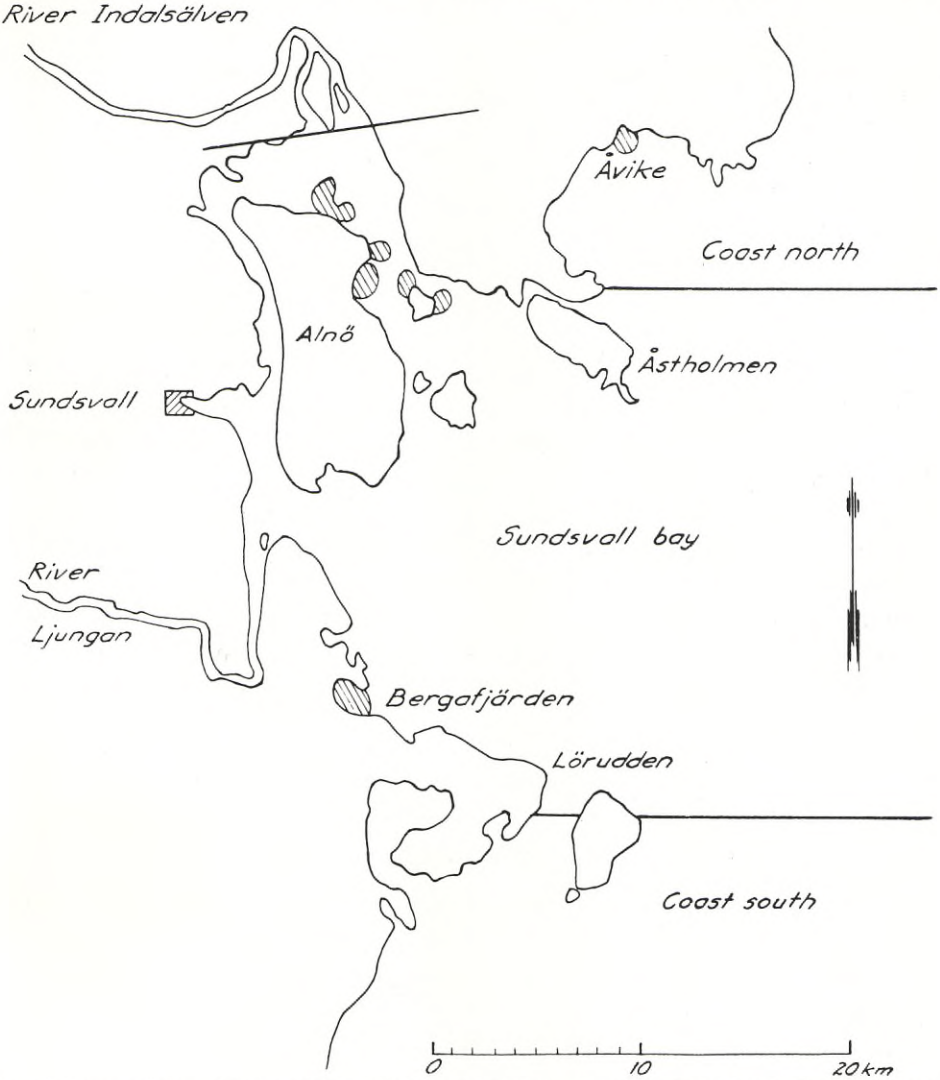

Fig. 3. Map of the Sundsvall bay district with known spawning places for *C. nasus*. Tagging return districts delimited.

b. *Results*

Table 3 comprises the data of the 15 tagging experiments 1951—1953 referred to in this paper. They may be summarized as follows.

	Tagged	Recaptured (until Oct. 1956) Nr.	p.c.
River spawning species *C. lavaretus*	712	144	20
Coast spawning species *C. nasus*	179	73	41
Coastal taggings of unspecified populations	401	159	40
Total	1,292	376	29

The map Fig. 3 shows the geographical boundaries of the regions of recapture referred to. The map Fig. 4 shows recaptures from the coastal area outside the Sundsvall bay.

1. Taggings on specified populations

α. Movements of *C. lavaretus*

During migrating time, before spawning, 568 specimens were tagged in the river giving 23 p.c. return. If the fish recaptured in the same fishing season are disregarded the return is 16 p.c.

During spawning time 144 specimens were tagged in the river. Of the two taggings in question recaptures up to only 2 and 12 p.c. have been reported in all, 0 and 10 p.c. the year after tagging.

As compared with the taggings on the coast the river taggings have on the whole given very small returns, especially the late taggings. It seems probable that in fresh water the spawning act or the tagging procedure, or both, put a stress upon the fish which causes a low survival ratio. This would agree with known experiences of salmon fresh from the sea. It may be observed that the taggings on spawning *C. nasus* by the coast give excellent return figures.

This explanation of the low return figures for *C. lavaretus* being given, the group of 144 returns may be treated as a whole.

Of the recaptures 62 were made in Indalsälven that is 43 p.c. (of the recaptures). Of these 48 that is 33 p.c. were made in the same year as the tagging.

No recaptures are reported from other rivers.

In the Sundsvall bay the tagged fish are caught mainly in spring or early summer — earliest reported Febr. 2nd — 35 (24 p.c.) one to three years after the tagging. Very few are taken here in autumn, and then mostly in September.

On the coast north of Sundsvall bay a few tagged fish, 9 that is 6 p.c., were taken in the spring or summer. To the south of the bay, on the other hand, many returns were made, 33 (23 p.c.), mostly in spring or early summer 50—100 km from the mouth of the river. The longest journey extended, as far as is revealed by recaptures, about 200 km, to the southern limit of the Bothnian Sea.

There seems to exist in the adult fish after spawning a quite regular mainly southwards-directed coastal migration changing during summer into a northwards-directed spawning migration. Most probably this journey is made every year, the members of the species gathering in their home river, or there would have been more autumn returns from the coast and the outer Sundsvall bay where the fishing continues to this time.

Table 3. Tagging experiments.

Taggings				Recaptures														
Population and place	Ser. nr.	Date	Nr.	Indalsälven														
				T			T+1			T+2			T+3			T+4		
				I	II	III	I	II	III	I	II	III	I	II	III	I	II	III
Coregonus lavaretus																		
Småholmarna, river Indalsälven	1951: 3	4—19/9 -51	71	—	5	1	—	—	—	—	2	1	—	—	—	—	—	—
Östloning » »	1951: 8	16/11 -51	51	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Bogrundet » »	1952: 4	28/8—17/9 -52	112	—	15	3	—	—	1	—	—	1	—	—	1	—	—	—
Måsgrundet » »	1952: 5	1—18/9 -52	385	—	15	7	—	2	2	—	1	—	—	2	—	—	—	—
Östloning » »	1952: 13	21/11 -52	93	—	—	1	—	—	—	—	—	—	—	1	—	—	—	—
		Sum	712	—	35	13	—	2	3	—	3	2	—	3	1	—	—	—
Coregonus nasus																		
Slädaviken, Alnö	1952: 11	22/10 -52	50	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
» »	1953: 11	29/10—3/11 -53	129	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
		Sum	179	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Unspecified population																		
Härnön	1953: 2	27/5 -53	30	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—
Barsviken	1953: 3	27/5 -53	60	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
Spikarna	1951: 4	5—7/9 -51	42	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—
Lörudden	1951: 1	22—29/8 -51	50	—	5	2	—	1	—	—	—	—	—	1	—	—	—	—
»	1952: 2	17/6 -52	42	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—
»	1952: 7	17—18/9 -52	47	—	—	4	—	2	1	—	—	—	—	—	—	—	—	—
»	1953: 4	9/6 -53	40	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Ragvaldsnäs	1951: 2	29/8—12/9 -51	50	—	—	3	—	—	1	—	—	—	—	—	—	—	—	—
Jättholmarna	1953: 5	17/6 -53	40	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		Sum	401	—	6	14	1	4	2	—	1	—	—	1	—	—	—	—
		Total	1292															

Population and place	Ser. nr.	Sundsvalls bay														
		T			T+1			T+2			T+3			T+4		
		I	II	III	I	II	III	I	II	III	I	II	III	I	II	III
Coregonus lavaretus																
Småholmarna, river Indalsälven	1951: 3	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—
Östloning » »	1951: 8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bogrundet » »	1952: 4	—	—	—	4	2	—	—	2	—	—	—	—	—	—	—
Måsgrundet » »	1952: 5	—	3	—	8	2	1	2	1	—	1	3	—	—	—	—
Östloning » »	1952: 13	—	—	—	1	1	—	—	2	—	—	—	—	—	—	—
Sum		—	3	—	14	6	1	2	5	—	1	3	—	—	—	—
Coregonus nasus																
Slädaviken, Alnö	1952: 11	—	—	6	1	2	2	1	1	—	—	1	—	—	—	—
» »	1953: 11	—	—	16	6	7	9	—	3	3	—	—	—	—	—	—
Sum		—	—	22	7	9	11	1	4	3	—	1	—	—	—	—
Unspecified population																
Härnön	1953: 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Barsviken	1953: 3	—	1	—	—	4	1	—	1	—	—	—	—	—	—	—
Spikarna	1951: 4	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—
Lörudden	1951: 1	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—
»	1952: 2	—	11	1	2	1	—	—	—	—	—	1	—	—	1	—
»	1952: 7	—	—	—	2	3	—	—	—	1	—	—	—	—	—	—
»	1953: 4	—	6	3	3	7	—	—	—	—	—	—	—	—	—	—
Ragvaldsnäs	1951: 2	—	—	3	—	2	—	—	1	—	—	—	—	—	—	—
Jättholmarna	1953: 5	—	—	—	1	—	—	—	3	—	—	—	—	—	—	—
Sum		—	18	7	11	18	1	1	5	1	—	1	—	—	1	—

Population and place	Ser. nr.	Coast northwards														
		T			T+1			T+2			T+3			T+4		
		I	II	III	I	II	III	I	II	III	I	II	III	I	II	III
Coregonus lavaretus																
Småholmarna, river Indalsälven	1951: 3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Östloning » »	1951: 8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bogrundet » »	1952: 4	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—
Måsgrundet » »	1952: 5	—	—	—	1	2	—	2	1	—	—	—	—	1	—	—
Östloning » »	1952: 13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sum		—	—	—	1	3	—	2	1	—	—	—	—	1	—	—
Coregonus nasus																
Slädaviken, Alnö	1952: 11	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
» »	1953: 11	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Sum		—	—	—	1	—	—	—	—	—	—	1	—	—	—	—
Unspecified population																
Härnön	1953: 2	—	4	—	1	4	—	—	1	—	—	1	—	—	—	—
Barsviken	1953: 3	—	3	4	—	1	1	—	2	—	1	—	—	—	—	—
Spikarna	1951: 4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lörudden	1951: 1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
»	1952: 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
»	1952: 7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
»	1953: 4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ragvaldsnäs	1951: 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Jättholmarna	1953: 5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sum		—	7	4	1	5	1	—	3	—	1	1	—	—	—	—

Population and place	Ser. nr.	Coast southwards															unknown	Total	
		T			T+1			T+2			T+3			T+4				Nr.	p.c.
		I	II	III	I	II	III	I	II	III	I	II	III	I	II	III			
Coregonus lavaretus																			
Småholmarna, river Indalsälven	1951: 3	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	13	18
Östloning » »	1951: 8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
Bogrundet » »	1952: 4	—	—	—	2	1	—	3	1	—	—	—	—	—	—	—	—	38	34
Måsgrundet » »	1952: 5	—	—	—	11	4	—	4	—	—	—	—	—	—	1	—	4	81	21
Östloning » »	1952: 13	—	—	—	—	—	—	1	2	—	1	—	—	—	—	—	1	11	12
Sum		—	—	—	13	6	—	9	3	—	1	—	—	—	1	—	5	144	20
Coregonus nasus																			
Slädaviken, Alnö	1952: 11	—	—	—	3	—	—	2	1	—	—	—	—	—	—	—	—	21	42
» »	1953: 11	—	—	—	1	3	—	—	1	—	—	—	—	—	—	—	1	51	40
Sum		—	—	—	4	3	—	2	2	—	—	—	—	—	—	—	1	73	41
Unspecified population																			
Härnön	1953: 2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1	15	50
Barsviken	1953: 3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	21	35
Spikarna	1951: 4	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	7	17
Lörudden	1951: 1	—	—	1	3	—	—	—	1	—	—	—	—	—	—	—	2	19	38
»	1952: 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	21	50
»	1952: 7	—	—	—	2	2	—	1	—	—	1	—	—	—	—	—	—	19	41
»	1953: 4	—	1	—	—	2	—	—	—	—	—	—	—	—	—	—	1	24	60
Ragvaldsnäs	1951: 2	—	—	—	3	3	—	—	1[1]	—	—	—	—	—	—	—	2	17	34
Jättholmarna	1953: 5	—	5	1	3	2	—	—	1	—	—	—	—	—	—	—	—	16	40
Sum		—	7	2	11	10	—	1	4	—	1	—	—	—	—	—	7	159	40
Total																		376	29

T = Tagging year. I = Jan.—May, II = June—Sept., III = Oct.—Dec. [1] Recapture at Kaskö, Finland.

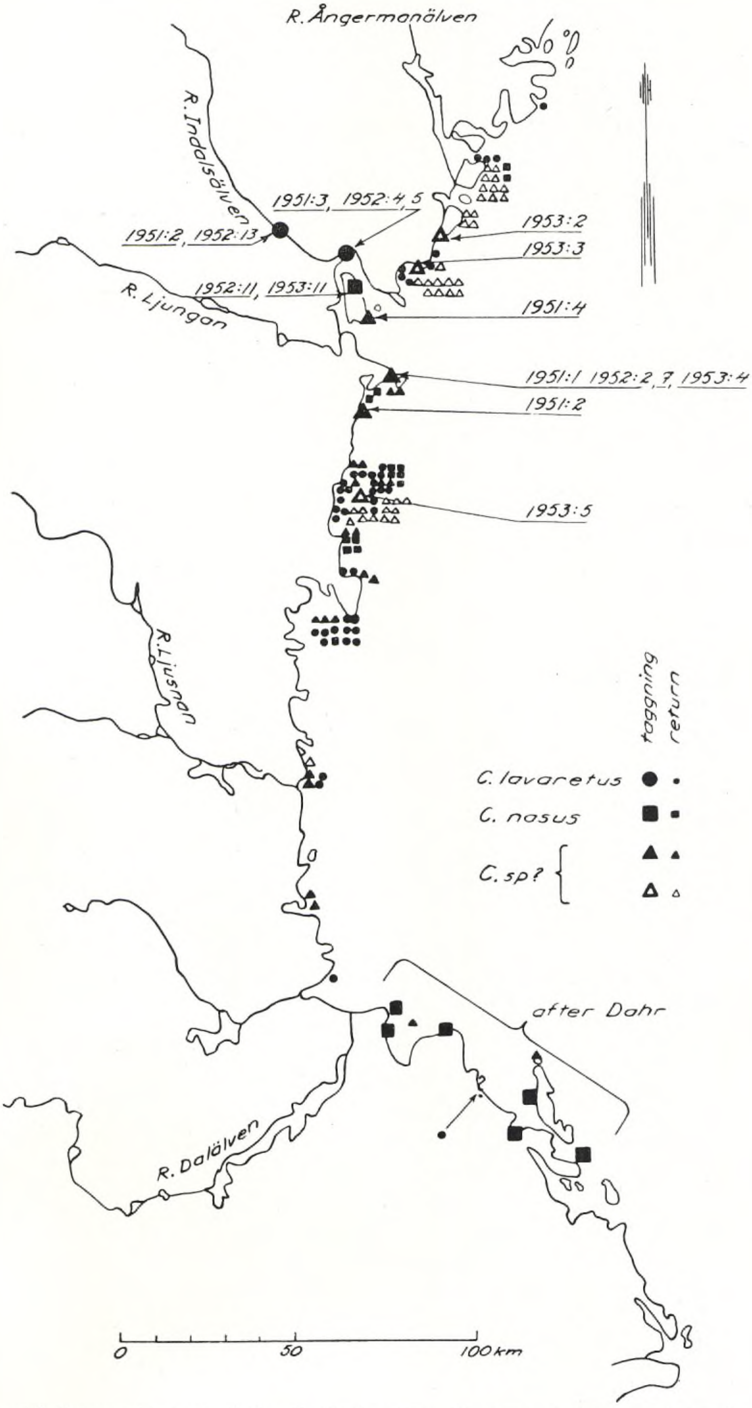

Fig. 4. Map of the west coast of the Bothnian Sea. Tagging stations and tagging returns outside the Sundsvall bay indicated. Tagging returns from the taggings of Dahr (1947) are not considered.

β. Movements of *C. nasus*

At the spawning grounds at Alnön close to the mouth of Indalsälven 179 specimens have been tagged in two consecutive spawning seasons. The total return was 73 specimens or 41 p.c.

In the river Indalsälven one specimen has been found.

The large majority, 58 specimens or 79 p.c. (of the returns) was taken in the Sundsvall bay mostly close to the tagging place in the year of tagging or the year following.

One fish has migrated to the north and 11, that is 15 p.c., southwards, one specimen as far as about 90 km.

The taggings on specified populations seem to reveal about the same migratory habits in both of the species: a gathering to the spawning areas in autumn, dispersing along the coast mainly southwards in spring (possibly as early as winter) after the spawning and a return to the spawning grounds in the autumn. That it is not a question of a circular more or less passive migration along the coasts of the Bothnian Sea in the anticlockwise direction of the prevalent currents of this enclosed section of the Baltic is clear from Fig. 5. Those fish recaptured to the north and to the south of the bay are conformly distributed in time without any sign of a southgoing emigration in early summer or a corresponding return from the north later in the summer or in the autumn.

The river spawning *C. lavaretus*, however, seems to be a more typical migrating species than *C. nasus*. It travels further both to the north and to the south and is taken outside of the Sundsvall bay to a greater extent, as is made clear by the following table. (The recaptures made in the year of tagging are omitted because they depend to a large extent on the actual fishing effort at or near the tagging place after the date of tagging.)

Species	Tagged	Recaptures after the year of tagging total	river a. bay	coast north	coast south
C. lavaretus	712	88	46 (52 p.c.)	9 (10 p.c.)	33 (38 p.c.)
C. nasus	179	49	36 (74 p.c.)	2 (4 p.c.)	11 (22 p.c.)

It is probable, as already mentioned in the case of *C. lavaretus*, that the greater part of the populations of both species return for spawning after only one year but it is reasonable to assume that exceptions exist.

2. Taggings on unspecified populations

Tagging (1953:2) at Härnön to the north of Sundsvall bay was undertaken on a population possessing, according to the returns, a weak contribution of the river spawning species. The returns of tagged true *C. lavaretus* on the other hand have, as mentioned above, in consequence revealed that their connections with the northerly populations are not intimate.

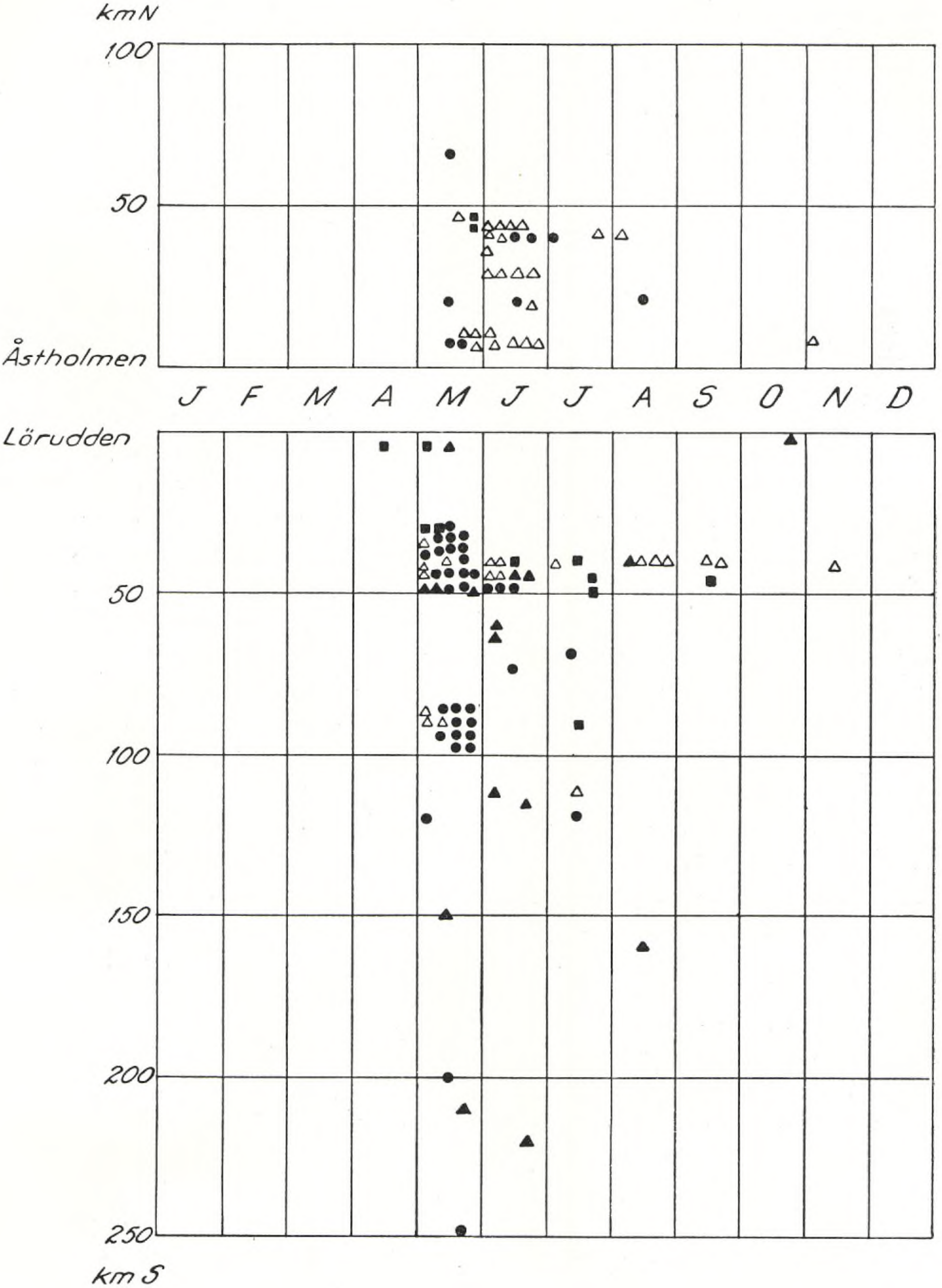

Fig. 5. Distances of tagging returns of whitefish north and south of the capes demarkating the Sundsvall bay, plotted against time of year. For explanation of signs see Fig. 4.

The same is true of the (1953: 3) tagging a little more to the south. Several recaptures, however, were made in the Sundsvall bay.

Only one specimen of the northern populations has gone south beyond the Sundsvall bay.

The taggings at Lörudden (1951: 1, 1952: 2 and 7, 1953: 4), the southern limit of the Sundsvall bay, give returns according to the season of tagging.

		Recapture			
Tagging season	Tagged	total	river	bay	coast south
June (1952: 2, 1953: 4)	82	42	3 (7 p.c.)	36 (86 p.c.)	3 (7 p.c.)
End Aug.-Sept. (1951: 1, 1952: 7)	97	36	16 (45 p.c.)	9 (25 p.c.)	11 (30 p.c.)

The populations tagged here in June appear, to judge from the above table, to contain a smaller proportion of the river migrating species than do the autumn populations which, like *C. lavaretus*, contain more southwardly migrating specimens. It is thought, if we dare generalize from the results of those few taggings, that *C. lavaretus* as a more typical migrating fish, passes the Lörudden cape in a southerly direction in the spring, before the intense fishing sets in, and is relatively sparse in the bay during summer until the return migration has started. A further indication of the difference between the populations is this — that of the June tagged fish, 4 were retaken in the bay at spawning time some of them on the spawning grounds, whereas this is the case for only one fish tagged in the autumn.

The tagging experiment further to the south (1951: 2) which was carried out in late summer gave two recaptures at spawning time, both in Indalsälven, where two more were taken before the spawning season. The character of the population tagged seems to be the same as those of the late season taggings at Lörudden. One specimen is reported as far to the south as Uppland (nearly 200 km away) and one from Kaskö in Finland (200 km distance east of the tagging place).

The tagging made furthest to the south at Jättholmarna (1953: 5) in June gave 30 p.c. returns from or near the place of tagging and 10 p.c. from the Sundsvall bay. The population seems to be rather stationary as compared with the other populations investigated.

It is worth noticing that no specimen tagged to the south of the Sundsvall bay (including Lörudden) passed the bay northwards.

c. *Discussion*

Taggings of whitefish in the Baltic area have up to now been published only by **Dahr** (1947), from the southern part of the Bothnian Sea. In the last few years taggings have also been carried out in the northern part of the Bothnian bay but concerning these no informations have so far been published.

Dahr, having tagged 393 whitefish at 6 different places (see Fig. 4), probably exclusively from *C. nasus* or the coast spawning species, and having obtained 158 recaptures mostly from neighburing localities (mean apparent distance of travel 8—9 km), concludes that in all likelihood the local populations keep in the proximity of the special areas used as their spawning grounds and are to a certain extent isolated from one another.

The experiments of the present author at Härnön to the north of Sundsvall bay and at Jättholmarna to the south do not, generally speaking, differ to much from the results arrived at by DAHR. It seems plausible to assume that the west coast of the Bothnian Sea, to restrict the discussion to this area, is inhabited by fairly local populations of *C. nasus* scattered around their coastal spawning areas to which they concentrate in autumn. Populations belonging to the river spawning *C. lavaretus* break through this chain of *C. nasus* in the spring or perhaps earlier in the winter when they leave their home rivers as spent fish and disperse in the coastal waters showing a clearcut tendency to a southerly directed migration which in some cases may extend as far to the south as that part of the coast where DAHR tagged his fish. This migration changes during the summer into a definite spawning migration culminating in late summer and early autumn.

The nature of the demonstrated differences in migration is obscure. It may be that they are founded in genetically different reactions to external influences but the possibility remains that the entire difference is to be found in the hydrological conditions encountered by the fry. As shown below the fry of *C. lavaretus* is swept passively out of the river by the stream. The general direction of the outstreaming Indalsälven freshwater in the sea is southerly (LINDROTH 1953 a and b) and it is very likely that the fry is passively carried along with this current. The risk of such an occurrence is very much smaller in the case of the *C. nasus* fry hatched on the spawning places in the coastal bays. Therefore, from the beginning of their swimming life, the individuals of the two species are faced with different external conditions which might give the solution, or part of it, to the observed differences in migratory behaviour.

The populations of *C. nasus* at Alnön, close to the river mouth reveal as to their migratory habits a character intermediate between *C. lavaretus* and the populations of *C. nasus* studied by DAHR and similar populations tagged by the present author at the limits, to the north and to the south, of his area of investigation. Though some sort of direct influence may exist — a restricted exchange of genes in not inconceivable (cf papers by SVÄRDSON) and the formation of mixed shoals is likely to occur[4] — it is perhaps a simpler explanation, and agrees with the hypothesis put forth above, to consider the proximity of the spawning places of the Alnön populations to the river water currents in the sounds east of Alnön.

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[4] SVÄRDSON (1953) speaks of "shoaltrapped" whitefish. The keeping together of individuals in a whitefish shoal for at least 5 years is shown by KENNEDY (1954).

It may by stressed here that the extension of the normal migration area, or stretch of coast, of a population is not necessarily indicated by a few recaptures very far from the home of the population. On the contrary these may be erring specimens who after extended or wrongly directed migration fail to find their way back again. This question ought to be studied by releasing recaptured fish for a second recapture an investigation demanding very extensive taggings and extremely good contact with those fishermen likely to catch tagged fish at the limits of migration.

The tagging experiments reported here may throw some light upon homing behaviour in whitefish. As clear from the table below no specimen of *C. lavaretus* from Indalsälven was ever recaptured in any other river[5] and at spawning time only one was reported from the bay outside the mouth of Indalsälven. Of *C. nasus* no return is known from any other part of the bay than Alnön during spawning time, though at least one more spawning place is situated in the bay. This is strongly indicative of a homing behaviour in the whitefish populations under consideration.

		Recapture at spawning time after the year of tagging		
Species	Spawning place	total	Indalsälven	bay (Alnön)
C. lavaretus	Indalsälven	7	6	1
C. nasus	Alnön	14	—	14

It may be pointed out that the homing behaviour has, so far, been discussed only in adult fish returning for a second (or third etc.) time to the spawning areas where they were tagged. Concerning the homing of fry and young fish nothing is known although investigations have begun.[6]

The tagging material is to sparse to permit conclusions as to differences in migration directions and extensions from year to year, though such differences are indicated. A warning against generalizing from the results of a few years seems appropriate. The question will be followed up through yearly taggings of *C. lavaretus* in the river.

Migrations of whitefish are reported from other European and American populations and as pointed out by WAGLER (1941) the migratory urge obviously runs in the salmonoid families. (See also SCHEURING 1929, KENNEDY 1954.)

III. Spawning

a. *Sex ratio*

The primary sex ratio in fry or very young fish was not investigated. As, however, the actual sex ratio found in adult fish in the catches from the coast

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[5] Throughout the investigation no recapture was reported from any other river than Indalsälven not even from Ljungan which empties into the same bay. Of 96 returns from coastal taggings to the south of Sundsvall bay 22 have been made in Indalsälven and none in Ljungan. Although the whitefish fishery of this river is not nearly so intense this fact is astonishing.

[6] In Sept. 1956 900 one summer old young have been tagged and liberated in Indalsälven.

outside spawning time (Table 1, Appendix) differs only slightly from the 50 : 50 ratio it seems probable that these figures hold true for the primary sex ratio. About 50 : 50 ratio is given also for other European coregonids and for the American *C. clupeaformis* (see WAGLER 1941, VAN OOSTEN 1939, VAN OOSTEN and HILE 1949).

The catches of migrating and spawning fish differ from the ratio given above. All catches of *C. lavaretus* in early autumn show a clear preponderance on the part of the male fish[7] whereas the females dominate in the samples taken at spawning time both with *C. lavaretus* in the rivers and *C. nasus* in the coastal waters (with one exception). The experiences of the fishermen licensed to take spawning fish in the river seem to show that seine nets worked over the spawning grounds give a majority of males while other catches give more females.

The differences observed correspond to behaviour patterns in the sexes varied according to the sexual year cycle of the fish not studied here in detail. An earlier ascending of the river on the part of the males, during the open season (ending Oct. 1st) seems probable. In the same way the males are believed to occupy the spawning grounds in advance of the females and remain there for a long time receiving shorter visits from the ripe females staying in the vicinity of the grounds.

This behaviour on the spawning grounds is known from other whitefish populations and appears to be the general rule (SCHEURING 1929, WAGLER 1941). The same tendency on the part of the males prevailing on the spawning grounds is evident also from Swedish investigations (DAHR 1947, TOOTS 1949).

b. *Spawning grounds*

C. lavaretus, the river spawning species, spawns on the stony and gravelly bottom in those parts of the river having a faster stream and also on the gravelly and sandy grounds where the water flows more slowly. (For a description of the river see LINDROTH 1955.)

C. nasus prefers the stony grounds of secluded coastal bays. No special investigation was carried out, the map, Fig. 3, showing only the approximate situation of the spawning grounds known to the local fishermen.

c. *Spawning time and spawning age*

C. lavaretus in Indalsälven begins to spawn in the first half of November. The water temperature at that time varies between about 1 to 3° C. The spawning activities of the population last for about one month.

C. nasus spawns earlier, from about the middle of October. Temperatures at the spawning places have not been recorded.

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[7] The dominance of the males in the spawning run of *C. clupeaformis* has been shown by VAN OOSTEN and HILE 1949.

The question of the connection between spawning time and water temperature and the consequent shifting of spawning time in differing years and in differing areas along the Baltic coast will not be discussed in this paper. (See FABRCIUS 1950, SVÄRDSON 1953.)

The smallest adult fish in the samples from the commercial fishery were 26—28 cm total length, 5 years old and ready to spawn. This case was the same for both species. This age is by no means the minimum age for sexual maturity. DAHR (1947) reports sexually mature males of 2 years (cf. also WAGLER 1941) but he has studied a very quickly growing population.

The tagging experiments indicate that at spawning time the whitefish rarely stay outside the spawning area of their population. Of the catches of whitefish which have been examined, those from autumn migration or those taken at the spawning places in late autumn, contain almost exclusively fish ready to spawn in the same season (cf VAN OOSTEN and HILE 1949). It is concluded that the vast majority of the whitefish having once attained sexual maturity spawn every year. Exceptions however may exist (cf. Rosén 1920).

d. *Spawning activities and fertilization (C. lavaretus)*

During spawning time a loud splashing is to be heard about the spawning grounds in the river at dusk and nightfall and has long been rightly believed to be connected with the spawning activities of the whitefish. Following the study of the spawning behaviour of *C. lavaretus* from Indalsälven (FABRICIUS and LINDROTH 1954) it is clear that the splashing noise is brought about by the mating couples reaching the water surface in the last convulsive movements of their copulation.

On the river bottom the fish swim restlessly around, and then by the fall of darkness are stimulated to greater activity. A kind of display is followed by rushes towards the surface both singly and in couples. In a complete act a male approaches the female and the couple rush side by side towards the surface performing simultaneous undulatory movements and giving off their sex products. In a successful copulation 50—100 eggs are ejected. (This description after FABRICIUS and LINDROTH 1954.)

The emitted eggs sink down through a suspension of sperm. During the short time of contact the micropyle must be found and invaded by a spermule, because of the short fertilization time of the sex products of both sexes. This time, although not studied in the case of the whitefish, may be supposed to be of the same duration as in the case of the small whitefish, *C. albula* (see LINDROTH 1946 b), viz. c. 2 min. according to the temperature.

The efficiency of the fertilization was not studied in this investigation but was found by TOOTS (1949 a and b) to be 89, 98, 99 and 100 p.c. respectively in 4 samples from a stream spawning population. Lake spawning whitefish too reach high fertilization values (probably 95 p.c. and more, see WAGLER 1941).

e. *Number of eggs*

The number of eggs of *C. lavaretus* has been investigated in the case of the Indalsälven population (JOHANSSON 1956). It is found to amount to about 20,000 pr kg of female fish and no correlation seems to prevail with the size of the individual fish within the population. TOOTS (1949 a) communicates figures for "blåsik" (probably the same species as the *C. lavaretus* treated in this paper); the mean number per kg of fish is 23,000 with an inverse correlation between fish size and egg number per kg. Records on egg number and egg size in other whitefish species and populations are given by OLOFSSON (1933), ELSTER (1934), WAGLER (1941) and TOOTS (1951). The figures vary between 15,000 and 58,000 pr kg of fish.

f. *Discussion*

The two species of Coregonus show obvious differences in regard to their spawning habits. *C. lavaretus* spawns in streaming water, over stony or gravelly ground and comparatively late, *C. nasus* in quiet water, over stony bottom and comparatively early. FABRICIUS (1950) has, however, warned against paying too much attention to differences in spawning time without a close study of local temperatures. The difference in time may be due to differences in temperature, the reactions of maturing and spawning fish remaining the same in the two populations. The same argument can be extended to the discussion of spawning place. The type of bottom is roughly the same (cf. FABRICIUS 1950) and may be the determining factor. The hydrological conditions, which give the localities such differing characters to the human eye, might be of inferior importance to the spawning fish. The reactions of the fish may be assisted by a homing behaviour, and in this connection it is of interest to note that on account of the continuing post-glacial marine regression the present spawning areas of *C. lavaretus* in Indalsälven were, during the so-called *Ancylus*-stage in the history of the Baltic some 7,000 to 9,000 years ago when whitefish were known to live in Sweden (EKMAN 1922), covered by the water of the *Ancylus*-lake. The idea of an originally lake spawning whitefish holding on to a spawning area gradually shifting into a stream is suggestive.

To conclude, the differences observed in the spawning of the to species constitute no evidence of genetical differences in reactive behaviour of the fish.

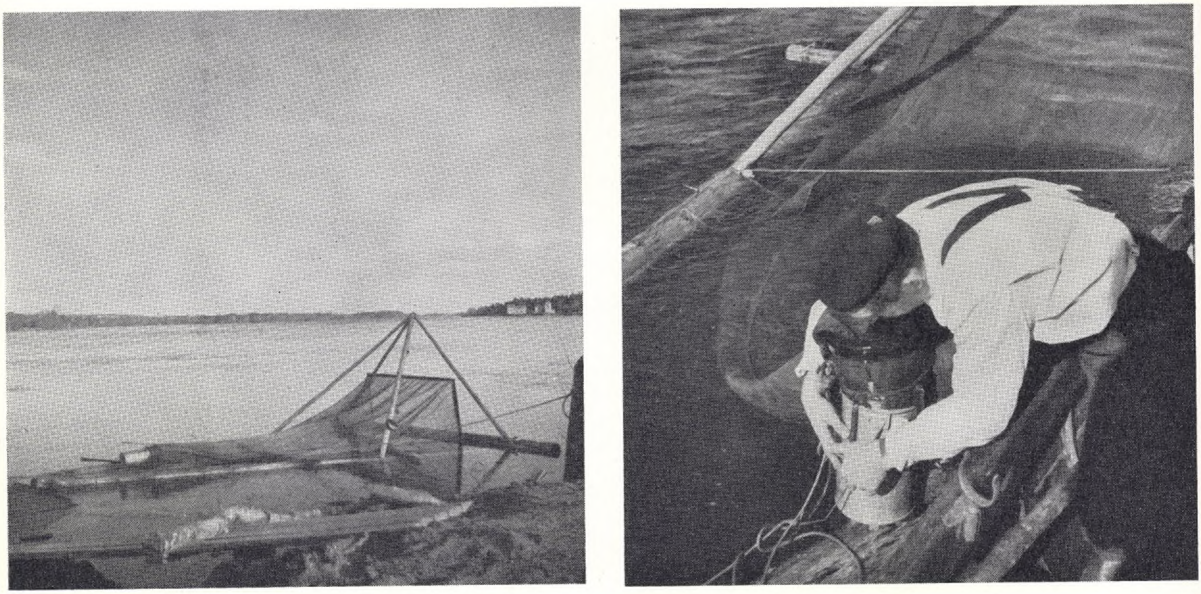

Fig. 6. The whitefish fry net. — Photo: H. PETERSON.

IV. Biology of egg, fry and young of *C. lavaretus*

a. *Methods*

1. Trapping of eggs. A small anchored dredge with triangular frame, 30 cm sides, and a nylon net of 1 mm mesh was used for investigations of the bottom drift of the river. A conventional bottom sampler (EKMAN type) was used for taking samples of the deeper sea bottom.

2. Trapping of fry. The stream drift has for several years been sampled by means of a large nylon net, frame opening 200×100 cm, length 500 cm, fastened to an iron frame suspended from a log float in the lower part of the river (see Fig. 6). Owing to variations in the velocity of the stream, clogging by detritus, and other imperfections, the daily catches are only roughly quantitative. (Detailed records of the fry net operations are to be found in LINDROTH 1953 c, 1954 a, JOHANSSON 1956 b.)

During field excursions the fry observed was caught with various types of small dip nets, no easy task, and one demanding much training and swiftness on the part of the fisher. The operation was best performed as a single stroke from above.

3. Trapping of young. Young whitefish are now and then caught at the commercial fishery in the river with seines, and some fishermen were equipped with jars and formalin for the preservation of any small fish they might take. In a few instances a special finely meshed seine was used.

Table 4. Catches of drifting whitefish eggs in river.

Date	Locality km fr. mouth	Catching time, days	Eggs	Eggshells	Coniaments
21 Nov. 1952	33	1	11	—	1 *Trichoptera*
29 ,, 1952	33	8	15	11	
12 ,, 1952	10	1	1	—	Diff. insect larvae: *Plecoptera*, *Ephemeroptera*, *Trichoptera*, *Diptera*, *Corixa*, 1 *Ammocoetes*, 1 *Phoxinus*
13 ,, 1952	10	1	10	2	
14 ,, 1952	10	1	4	2	
15 ,, 1952	10	1	17	2	
18 ,, 1952	10	3	1	2	
24 ,, 1952	10	6	2	1	
25 ,, 1952	10	1	—	—	
26 ,, 1952	10	1	—	—	
29 ,, 1955	6	Several eggs, fertilization certified			
30 ,, 1955	6				

Large quantities of small young were taken in a salmon smolt trap near the mouth of the river. As far as these fish were concerned, this device worked as a 8—10 m wide funnel which concentrated shoals of drifting fish and guided them downstream into a large brass cage 300×300×100 cm. The entrance was blocked by a d.c. electric field which shocked the entering fish as well as fish trying to leave the trap.

4. Swimming speed experiments. Experiments to ascertain the swimming speed of fry were made in a aquarium 110×20×20 cm. A known flow of water was directed through the vessel either at a constant depth whereby the maximum flow withstood by the fry was recorded, or at an increasing depth and a consequently decreasing water velocity whereby the upstream swimming limit and theoretical water velocity were noted. Some experiments were carried out in a plastic tube 65 mm wide. In some of these experiments the intensity of the light was also varied.

b. *Results and special discussions*

1. The egg

The egg of the stream spawning whitefish is swept along by the currents as it sinks to the river bottom. Even after reaching the substratum it probably does not, as a rule, come to rest before rolling and drifting downstream for a considerable time. In our anchored dredges an extensive drifting of fertilized whitefish eggs along the bottom of the river has been clearly demonstrated (Table 4). The same is found for the smelt (see SCHEURING 1930 p. 252) and seems also to be the case with the shad (see MASSMAN 1952, TALBOT 1954).

It is concluded that only those eggs that become caught in holes and crevices between pieces of gravel and pebbles or happen to lodge in deeper pools — scarcely existing in this particular river — have a chance of developing in the river.

The newly spawned eggs take up water which increases their volume by 170 p.c. (JOHANSSON 1956) and they grow slightly sticky. Because of this the egg gradually becomes covered with small organic and inorganic particles, making them very difficult to detect in their natural site (as with pike, see LINDROTH 1946 a).

MONTÉN studying the biology of a lake spawning whitefish, proves that even under these conditions the eggs are easily swept away by water currents (MONTÉN 1948).

Several authors have stressed the heavy predation on the whitefish spawn. Most prominent of the predators is the whitefish itself and the burbot (ELSTER 1934, MONTÉN 1948, SEGERSTRÅLE 1947, own observations), in addition to other species of fish such as perch, millers thumb, and invertebrate animals (MONTÉN 1948, TOOTS 1949 a, SLACK 1955). MONTÉN studying a form spawning in shallow water gives the figure for supposed survival of eggs as low as about 0.5 p.c. (1948), and SLACK indicates a survival of eggs of *C. clupeoides* in Lock Lomond of 4 p.c. (1955).

In Indalsälven the combined action of predation and stream drift, none of which have been subject to detailed quantitative investigations, must cause a most serious reduction in the survival in the river of fertilized eggs, probably even greater than in MONTÉNS studies.

TOOTS (1949 a and b) has investigated the spawning ground of a stream spawning whitefish form and has taken living eggs in the lake below. In this case the eggs which are swept downstream by the current and which come to rest outside the stream, may still hatch and contribute to the reproduction of the population in question.

In Indalsälven the fate of the drifting eggs may be different. The shallow sandy bottom of the river delta falls steeply into a confined part of the Sundsvall bay, »Klingerfjärden», 53 m in its deepest part and connected with the outer bay through two sounds with threshold depths of 15—20 m. Hydrological investigations (LINDROTH 1953 a and b) show that the Klingerfjärden, immediately beneath the stratum of fresh water from the river, consists of a relatively salt brackish water (about 5 p.m.). This last forms a reaction current, induced by the outstreaming fresh water, is forced up along the steep slope at the edge of the river bottom, and there united and mixed up with the fresh water. Depressions like Klingerfjärden filled with comparatively heavy water — and moreover in this case receiving the waste waters from several pulp mills — are usually characterized by a periodically low content of dissolved oxygen especially in the bottom contact layer. Samples taken on the slope from under the ice 8—9 March 1956, about 1 m above bottom at a depth of 25—30 m revealed oxygen values lower than

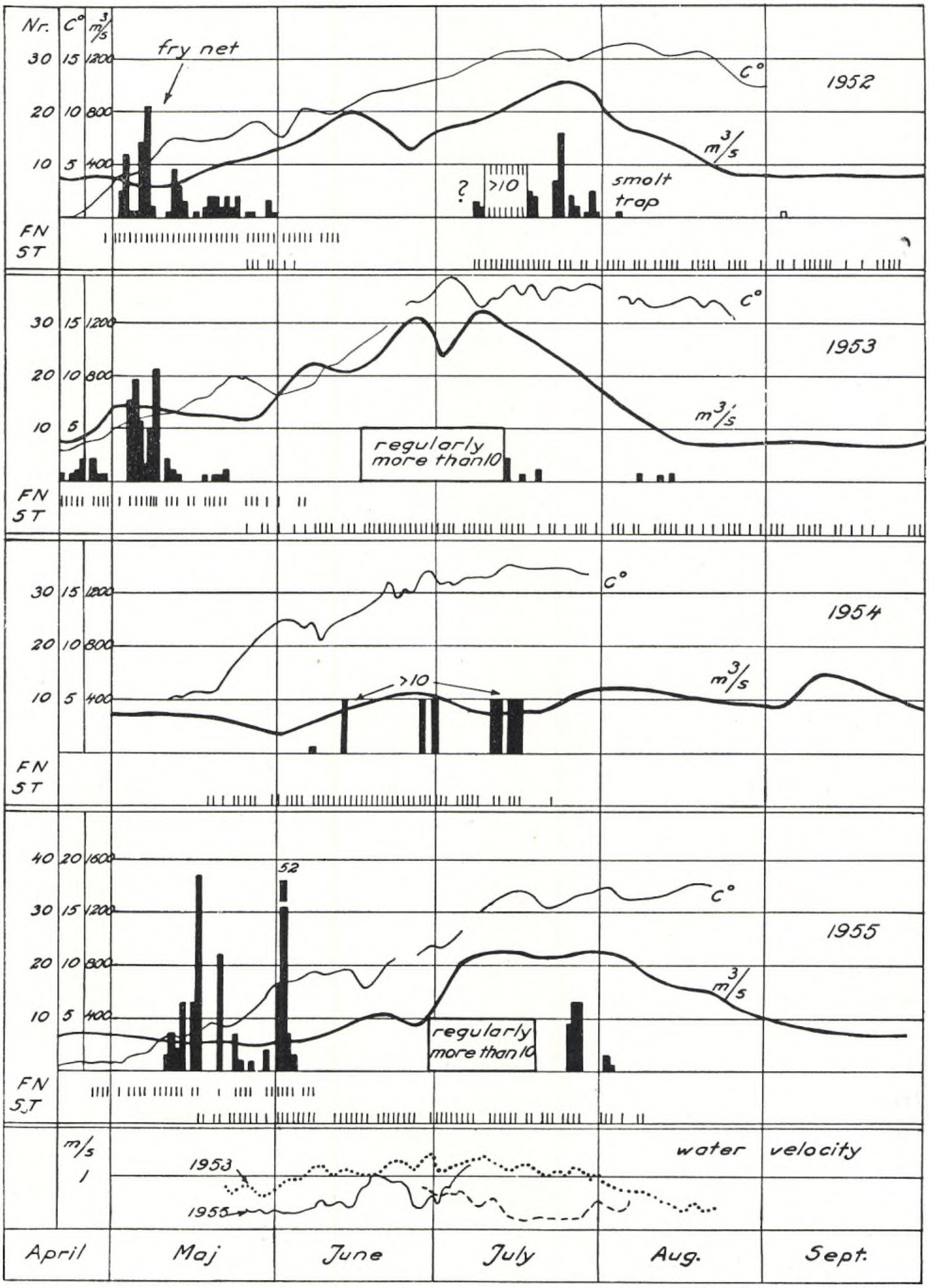

Fig. 7. Catches of juvenile whitefish in fry net and smolt trap in the mouth of river Indalsälven 1952—1955. Inspections of gear, smoothed trend of water temperature and flow indicated. Water velocity values below. FN=fry net. ST=smolt trap.

Table 5. Swimming speed experiments

Expt Nr.	Age of fry	t°C	Light	Observation
May 1952. Expts in rectangular vessel, oblique water surface				
1	0—3 d	6.5	Diffuse daylight	Mean water velocity at upstream limit of fry: 0.065 m/s
2	3—6 d	8.5	Dark night	All fry at downstream end at water velocities of 0.015—0.021 m/s
3	3—6 d	8.5	Weak from side	All fry distributed all over the vessel at the same water conditions as in expt 2
4	3—6 d	8.5	Weak at upstream end	Most fry in the upper end
5	3—6 d	8.5	Weak at downstream end	Most fry in the lower end
6	3—6 d	8.5	Strong light	All fry distributed
7	3—6 d	8.5	Strong light close to glass wall	Positive taxis
1953. Expts in tube				
8	0 d	7.5	Quite dark	Most fry in the lower end at 0.015—0.055 m/s
9	0 d	7.5	Scarcely perceptible light	Fry tend to distribute themselves upstream
10	0 d	7.5	Quite light	Fry evenly distributed at 0.06—0.07 m/s
11	0 d	7.5	Quite light	Fry tend to go downstream at 0.085 m/s
12	0 d	7.5	Quite dark 1 min	Fry in lower half of tube at 0.005 m/s

60—70 p.c. saturation. Still lower values must be encountered in the bottom contact where the eggs would lie after they had drifted out of the river, and these may have been fatal for the eggs. (For values of oxygen demand in eggs see LINDROTH 1942.) Existing data do not permit any definite conclusion but the author is inclined to believe that the eggs swept out of the river into Klingerfjärden would be lost, even apart from the predation factor.

2. The fry

α. Hatching

In the stream tank at the Hölle laboratory (LINDROTH 1954) where whitefish spawned in autumn 1952, one whitefish fry was seen in the following spring emerging from the bottom, swimming upwards only to be swept at once downstream by the water current. It is thought that the behaviour observed here is typical of the hatching of stream spawning whitefish. (Cf. SCHEURING 1929 p. 646.)

The hatching coincides with the biological spring of the river, i.e. the rise of the uniform winter temperature of the water. This fact is clearly demonstrated in Fig. 7. The appearance of fry in the fry net is linked with the temperature curve. The effect of a rising temperature on the enzymatic hatching processes is a wellknown fact (GRAY 1928, PRICE 1940, HAYES 1942) and very useful as a causal (proximate) factor for hatching in autumn and winter spawning fishes. In the Indalsälven the hatching, therefore, occurs at the end of April or the beginning of May.

β. Movement

Laboratory experiments. The swimming speed of the newly hatched fry was determined in the laboratory (Table 5). The experiments show that the fry are unable to orientate themselves in the dark and drift at the mercy even of very slow water currents. The slightest light, however, is perceived (the ordinary photometer was not so sensitive as the fry) and causes the fry to distribute themselves evenly in the water body of the experimental vessel up to a certain water velocity which they can not stand. This velocity was calculated to about 0.07—0.08 m/s.

The phototactic reactions were very interesting though not studied in detail. To a stimulus of weak light the fry respond by positive taxis. When a moving spotlight, in the otherwise dark room, was directed against the live tank containing thousands of fry it was possible to lead them all in a marching column. In diffuse light, on the other hand, the spotlight beam was avoided and made an empty channel through the mass of fry.

Field observations. After hatching, whitefish fry are frequently seen in the river. They appear single or in small shoals in the free water body (cf MELLEN 1923) perpetually swimming, as a rule against the current, with small rushes indicating feeding activity. They often maintain their position in relation to the underlying bottom.

The observations mostly refer to small eddies and bays. Now and then a fry or a shoal may get into the main stream only to be swept down the river.

The water velocity of the river proper is, in reality, far beyond the critical value for the swimming ability of the fry. Fig. 7 shows some measured values.

Results of the trapping of whitefish fry in the fry net in the main branch of the river delta are shown in Fig. 7. There exists a period of downstream migration, evidently passive, for about a month, probably with one peak. (The year 1955 is not representative of natural conditions, as most of the fry this year were liberated from a hatchery.)

The daily variation in the migration was investigated by 6-hourly catches May 16—17 1955. The main downstream movement seems concentrated around the darkest hours of the night both in whitefish fry and in newly transformed lampreys migrating in the same season.

		Content of net		
Date	Time	volume, l	whitefish fry	lampreys
May 16	1000	3	11	1
	1600	2	2	1
	2200	1	—	—
May 17	400	5	22	18
	1000	2	15	4

From the above it may seem evident that the hatching whitefish fry are normally carried downstream by the water currents immediately after hatching and swept out of the river, this downstream movement probably,

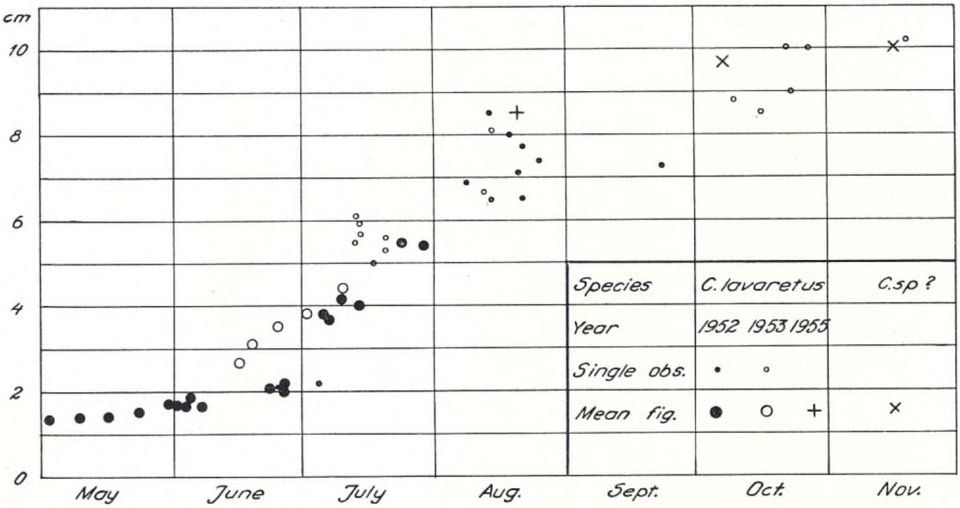

Fig. 8. Growth of whitefish during the first summer. River catches.

owing to the phototactic reactions of the fry, being most pronounced during the darkest part of the day. With a mean water velocity of 1 m/s a fry could under the most favourable conditions travel from the upper limit for the stream spawning species down to the coast, about 80 km, in one day. Eddies, small bays and quiet branches of the river may retain shoals of fry, some of them becoming gradually enclosed and killed in pools which dry up as the highwater retires. Sooner or later the surviving individuals reach the Sundsvall bay and the Bothnian Sea the brackish water of which is endured by the fry as shown by VALLIN (1936).

3. The young

α. Specifity and movements

As already mentioned not all the young leave the river as fry. Whitefish young of the 0-group are met with by the field observer in June—July and during the same period specimens were caught in small shoals in the smolt trap. Observations and catches indicate that the fish get sparser during the summer, and after July only solitary fish are taken (Fig. 7).

Statements from commercial fishermen indicated that shoals of larger young, 1—2 years old, were occasionally taken in the whitefish seines operated in the river in late summer and autumn. The opinion were often expressed that the river spawning whitefish, *C. lavaretus,* also grows up in the river.

The specifity of the young of whitefish in the river thus arises as an important problem.

The material of the 0-group fish from early summer (July incl.) originates

Table 6. Whitefish young from river Indalsälven 1 summer old or older (See fig. 1).

Date	Place	Age	Nr.	Length, cm	Gillrakers																Comments
					17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	
A. Upper part of river (45—75 km from mouth)																					
Oct. 1951	Korsåmon	1+	2	16									1		1						
,, 1951	,,	2+	1	21								1									
Nov. 1951	Liden	0+	6	9—11							1	2	2	1							
Aut. 1953	,,	0+	9	10—15						2	3	2	2								
,, 1953	,,	1+	2	20								1			1						
B. Middle part of river (15—45 km from mouth)																					
Oct. 1951	Tomming	1+	1	16						1											
,, 1951	,,	2+	1	21												1					
Sum			22							3	4	6	5	1	2	1					Mean 24.5
C. Lower part of river (0—15 km from mouth)																					
Sum. 1951	Bergeforsen	1+	2	13.5—16							1									1	
,, 1951	,,	2+	1	20.5							1										
Oct. 1953	Lövudden	1+	1	16.0							1										
,, 1953	,,		2	24—24.5										2							
Aug. 1955	Bergeforsen	0+	7	7.9—9.1						1						1	2	2	1		
,, 1955	,,	1+	4	12.9—19.8	1								1		1				1		
,, 1955	,,	2+	5	18.5—23.0				1	1					1		2					
,, 1955	,,	3+	1	22.1											1						
Nov. 1955	,,	4+	1	18.4																	38 gillr.
Aug. 1956	,,	0+	19	7.7—11.7							1	2	3	3		2	1	1	4	2	
,, 1956	,,	1+	7	12.3—17.5								1	3	1	2						
Sum			50		1	—	—	1	1	1	4	3	7	7	4	5	3	3	6	3	Mean 26.9
Total			72		1			1	1	4	8	9	12	8	6	6	3	3	6	3	Mean 26.2

almost exclusively from the smolt trap. The data from about 200 individuals are presented as the relation between the number of gillrakers and the size of the fish (Fig. 2) and between size and date of capture (Fig. 8).

The bulk of specimens seem approximately to fit the gillrakers curve approaching a definitive number of about 30. It would seem natural to attribute them to the river spawning *C. lavaretus* of the coast. However, aberrant numbers occur, a few individuals having more or fewer gillrakers than the majority. The possibility exists that these are of foreign origin.

Turning then to young fishes older than the July catches, Table 6 gives data of 72 whitefish young (one summer old or older) taken in different parts of the river. The mean number of gillrakers is 26.2 (a figure without value in this heterogenous population). Only 21 or 29 p.c. fall between 28 and 34 in which values 88 p.c. of true *C. lavaretus* fall. It is quite obvious from the data that only part of the whitefish young older than the 0-group in July can possibly belong to *C. lavaretus* spawning in the lower river. These last-mentioned young are found almost exclusively in the lowest 15 km of the river. The predominant category of the young fish is obviously that of trespassers with no domiciliary rights in this part of the river.

Whereas, therefore, the whitefish eggs swept out of the river must originate from the spawning of *C. lavaretus* in the lower part (0—80 km) of the river, and this is most likely true also of the fry taken in the fry net in May, probably holds good even with regard to the bulk — but not all — of the young taken in the smolt trap in June—July it is definitely untrue of the older young taken after this time. The question will be discussed below.

β. Growth

The growth of the river-caught young of supposed *C. lavaretus* is evident from Fig. 8. During their first summer of life the young attain a length of close on 10 cm. A differential growth according to varied water temperature or food conditions in different summers seems plausible but cannot be demonstrated from the material at hand.

γ. Food

The stomach content of some young from the 1952 and 1953 catches has been preliminary examined (Table 7). At a length of about 15 mm, when the yolk sac is only faintly visible, food is seen in the simple intestinal canal. At about 20 mm the intestine begins to coil.

The youngest fry feed mainly on copepods, chironomid and simulid larvae.[8]

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[8] Mellen (1923) reports the presence of four curved teeth in the lower jaw of fry of *C. clupeaformis* "which are of no possible service". Examination of fry of *C. lavaretus,* length about 18 and 35 mm, revealed no such teeth. Yet they ought to be very useful in seizing prey animals.

Table 7. Stomach contents of whitefish young in river 1952

Nr.	Date	Locality	Length, mm	Fish	*Ostrac.*	*Cop.*	*Clad.*	*Chironom.*		*Simulium*		*Plec. Ephem.*	Air ins.
								Larvæ	*Pupæ*	*Larvæ*	*Pupæ*		
1	May 25	River	14					5					
2			14					2		1			
3			14			1		3		1		1	
4			15					—		—			
5			15					1		2			
6			?					4		5			
7	Juni 1	River	14			10							
8			15			+		1					
9			15			+							
10			15			+							
11			16			+							
12			16			+							
13			16			+		1		2			
14			17			+		1					
15			18							1			1
16			18							1			
17			18			+				1			
18			18							1			
19			18			+				1			
20			19			5				2			
21			19			+		1					
22			19			+		2		1			
23			19			10—20				3			
24			20			++	1			1			
25	June 27	River	20						4	3			2
26			22					1	1			1	10
27			22					3		5			5
28			22						2	1			5
29	July 6	Enclosed pool	32			++		1					
30			33			+	+	1	1				
31			34			+	+	5—10					
32			37			+	+	2					3
33			38		1	+	+	2	4				
34			39			+	+	2					
35			40			++		1	2				1—2
36			40				+						1
37			43	2 fry		+		3	2				1
28	July 14	River	33					+					+
29			39					1		2			
30			40								2		+
31			41										+
32			46					2		22			
33			47										+
34			50					+		+			+
35			50					++		++			
36			52					1			1		
37			52										+

In older stadges later in summer air insects constitute a considerable part of the food. Wether this change corresponds to a change in preference or only reflects the availability of the food organisms has not been studied.

The food of the young, Nos 29—37, found enclosed in a quiet pool (cf. above), consists of organisms from the differing fauna in this place, viz. ostracods and cladocers.

The food of the young of an American stream dwelling whitefish (*Prosopium*) was found to be dominated by chironomid larvæ, pupae and adults besides mayfly larvæ and other minor constituents (length of young 30 and 50 mm mean in two samples). (LAAKSO 1951.)

LINDSTRÖM (1955), investigating the food of whitefish young in some northern lakes, has found copepods (in *Nauplius*-stage) in the youngest fry and later the cladocer *Bosmina*. Copepods are important also to the young of the pygmy whitefish in Lake Superior (ESCHMEYER 1955).

In the river the whitefish young growing up here feed on drifting animals, mainly dipterean larvae with which the river water abounds, as is clear from our investigations in Indalsälven (LINDROTH 1953 c, 1954 a, JOHANSSON 1956 b; cf. MÜLLER 1954). This type of food is biologically quite comparable to the true plancton of the lakes from the viewpoint of the most interested party, the whitefish young.

c. *General discussion*

In this discussion two problems will be dealt with: katadromesis in whitefish young and specifity of older young in the river.

1. Katadromesis

Before hatching, beginning as soon as spawning is over, there exists a passive downstream transportation of eggs. It seems a likely assumption that this phenomenon lacks any positive "purposeful" value for the maintenance of the population. With Indalsälven at least predation and adverse hydrographical conditions outside the river mouth strengthen this supposition though the case may be different in other places.

After hatching the following characters seem to be of importance in the effecting and timing of a seaward migration in whitefish.

1. Temperature control of hatching time. The developed embryo, ready to hatch throughout a certain period, manages to do so when the rising temperature has induced special unicellular glands to soften the chorion of the eggs. This mechanism, demonstrated in other fish (cf. p. 93), times the hatching to the rise in water temperature in spring, this interrelation being clear from Fig. 7.

2. Phototactic properties of the fry. Though only superficially studied such properties are very pronounced. They tend to keep the fry in the lighest part of the body of water, i.e. close to the surface.

3. Rheotactic responses. Relying upon visual stimuli the fry head upstream

against a moderate current to keep in the same place. In the dark their orientation is lost and even very weak currents displace the fry.

4. Shoaling behaviour. Shoals are readily formed as observed in the field and in traps.

5. Swimming properties. The fry is able to withstand a current of about 0.07—0.08 m/s in the light.

These facts result, in a habitat of streaming water, in a passive downstream mass transportation of newly hatched fry coming to a peak in the hours of darkness.

In every stream, however, habitats of varying size exist which are devoid of the streaming water characteristics. Behind stones on the bottom or by the bank, in eddies and bays and so on, quieter bodies of water may be found. Whereas positive phototaxis, I believe, tends to prevent the fry from lingering on the bottom and their liveliness to prevent them from staying in too small water bodies, larger eddies, yet, may retain shoals of fry as is seen in the field. These deleyed fish grow vigorous and become able to resist stronger currents, helped in this respect by the light of the summer nights in these latitudes. They form a rearguard which does not give way before the end of the summer when the river appears practically free from any whitefish young conceivably belonging to the studied *C. lavaretus* populations.

Between the mass transportation of fry, taken in the fry net, and the downstream migration of young caught in the smolt trap, there exists a gap difficult to explain by imperfections in trapping technique. At first it was thought that the fry alone represented *C. lavaretus,* the young originating from whitefish populations spawning in lakes and reservoirs further upstream in the water system. This hypothesis must however be abandonned (see below).

Though the appearance of whitefish young in the smolt trap was not closely followed up there seems to exist a connection between the rising water level in the river and the first appearance of the young in quantities. Prevailing material does not permit a definite conclusion but it is quite possible that a relative stability as regards contours of the shore and the bays inhabited by delayed whitefish fry shoals, is disturbed by a rising water level, which results in a new wawe of young transported downstream. (See Fig. 7.)

The downstream migration, divided into two different periods or not, is distributed over a considerable period. The migratory behaviour quantitatively most important for the maintenance of the stock of river spawning *C. lavaretus* I believe to be represented by the mass transportation of the newly hatched fry. The mechanism which prevents them from this early migration, seems to be working at random and the role played by the additional supply of the thus retained older young is difficult to ascertain. It is always unattractive to accept a very wide variation in behaviour or even two ways of behaviour as definitive means of attaining the one goal. Nothing tells us however that what we reveal of nature are in fact definitive solutions. The continuous selfadjustment of properties now at higher or lower levels of developement towards perfection seems a more proper framework of thinking — and in this case the stream spawning behaviour may well be a new departure (a question touched upon in other connections above) not yet followed by pertinent specialized behaviour as regards the downstream migration of young of these populations.

The katadromesis of stream spawning whitefish fry and young can be explained — from the evidence existing at the moment — as a merely passive transportation. This view entails one considerable advantage — there is no need to argue a differing behaviour pattern as compared with lake spawning populations. In artificial stream reservoirs, not to mention real lakes, most specimens are "delayed" throughout their life, and readily form self-propagating populations.[9] Fish rearing ponds of some size may be stocked with whitefish fry giving a high percentage of young in the autumn, though the meshes in the outlet gratings permit the fry to pass.

The downstream migration of river spawning whitefish demanding no special properties in the fish and no such properties having been developed in the course of evolution the apparent behaviour difference as compared with coast and lake spawning species is devoid of taxonomical value.

Downstream or seaward migration in fry and young of stream spawning fishes is especially well studied in salmonoids. According to HOAR (1953) young salmon may be divided into two distinct ethological groups: shoaling juveniles passively transported downstream and territorial juveniles where this transport takes place after a transformation into a smolt stage. HOAR indicates a negative rheotaxis in both groups. In atlantic salmon at least the smolt migration must be regarded as a very active behaviour and is being studied in current Swedish investigations (KALLEBERG, personal communication).

The behaviour of whitefish fry very much ressembles the general schema given by RUSSELL (1937) and HOARS description of chum and pink salmon (HOAR 1953) apart from the fact that special mechanisms for active downstream migration seem to have begun among the salmon species. Such mechanisms are evolved to a higher degree in connection with the smolt transformation in such species as exhibit this last. In the scale of mechanisms in juveniles of anadromous fish which secure the attaining of feeding places in lakes or, if lakes are passed, the sea, the *Oncorhynchus* and *Salmo* species and probably shad (see TALBOT 1954), lampreys and other fishes occupy various steps whereas *Coregonus* rests at the foot. It shares this humble position of lacking specialization with a great many fish normally regarded as devoid of stream migrating ambitions such as pike, perch, sticklebacks,

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[9] Cf. the case of a relict stream salmon (BERG 1953) discussed by SVÄRDSON (1955).

roach, as well as stream fishes like smelt and dace to mention, in the last groups, only fish migrating up the Indalsälven river system. It would seem proper, in this connection, to speak about obligatory as opposed to facultative anadromesis and katadromesis in fish.

2. Specifity of juvenile whitefish

The river Indalsälven has, for the years covered in this investigation, been accessible to the river spawning *Coregonus lavaretus* from the coast for about 80 km from the river mouth. The hatching fry drifts out of the river in May and a delayed portion leaves the river later in summer as shown above. Among the young, individuals of foreign origin are to be met with as early as in summer to judge from examination of the gillrakers (Fig. 2). With advancing age the proportion of foreign juveniles increases. In the upper part of the lower river stretch, no true *C. lavaretus* (i.e. of the coast populations) has ever been ascertained and in the lowest part they are few after the month of July as compared with other juveniles (Table 6).

The Indalsälven drainage area above the stretch accessible from the sea is inhabited by many differing whitefish populations. Fig. 1, prepared from data by SVÄRDSON (1953) and the present author (Table 1), illustrates 4 samples or groups of as many more or less homogenous populations from lake Storsjön together covering an amplitude in gillrakers from extremes 17—45. Two samples are taken in reservoirs in the headwater, and the combined gillrakers amplitude is 19—37. The selfpropagating population closest upstream of the river part accessible from the sea, lives in the Hammarforsen reservoir, mean gillrakers number in sample 25.1, amplitude 21—31.

Juvenile fish from the Hammarforsen reservoir exhibit striking differences as compared with the spawning fish. The mean gillrakers number in the sample was 26.5, the curve is twotipped and the amplitude amounts to 20—36. Now in the Gesunden reservoir some 35 km further upstream is found a whitefish population characterized by a higher number of gillrakers, mean 29.7. Whereas the majority of the young investigated most probably belong to the resident population part must derive from foreign populations most probably from the Gesunden whitefish.

Samples of juvenile fish from the upper and middle part of Indalsälven, about 15—75 km from the mouth of the river, where as far as known only *C. lavaretus* from the coast spawns, consist of individuals with gillrakers number 22—28, mean of 22 fish 24.5. There is every reason to believe them all to come from the Hammarforsen population.

Juveniles from the lowest part of Indalsälven constitute a very heterogenous group, amplitude in number of gillrakers 17—38. The two extremes, one fish in each case, lack analogues in the river populations sampled: not until lake Storsjön are whitefish with these figures to be found and the specimens in question in all likelihood originate from this lake. The mass of the young fish could, as far as gillrakers are concerned, belong to the Gesunden and the Hammarforsen populations. As however, only comparatively low number of gillrakers (as in the Hammarforsen populations) are found above this lowest part of the river it is thought that the stocking of Indalsälven with allopatric juveniles takes place mainly from the populations living nearest upstream. In this case a considerable part of the 50 young from the lowest river must be true *C. lavaretus* of the river spawning coast populations, the minute remains of the millions of fry swept out past here in May.

The downstream transportation of juvenile and adult lacustrine and fluviatile whitefish is not remarkable (see WAGLER 1941). In this case it is, rather, astonishing to note the contrary case inasmuch as only solitary individuals from the lake populations above Hammarforsen reservoir contribute to the young sampled below the dams. The bulk originate from the population domiciled in this reservoir, which was created by a power dam in 1928 and whose whitefish population most likely comes from a form in the lake Gesunden with a corresponding number of gillrakers (No. 21 in Table 1). There is every reason to believe that the new reservoirs in the river, which will soon be completely impounded down to 10 km from the mouth, will be stocked mainly from the Hammarforsen reservoir as the damming up of the river 10 km from the mouth was performed in autumn when no more young of the original populations can have possibly remained in the river.

The fate of the allopatric juveniles is obscure. More than 1,000 specimens of adult fish examined give no support to the idea that foreign individuals are to any noteworthy extent mixed with the shoals of the resident fish or live in the district. The problem will no doubt be dealt with in the course of SVÄRDSONs investigations, and is, therefore, left here.

V. Concluding remarks

Evidence of two species of *Coregonus* inhabiting the Sundsvall bay district is given from gillraker countings. No other morphological character has been investigated in detail.

Several differences in behaviour have been discussed. As already pointed out, however, the apparent divergencies in spawning habitat and in migratory habits in adult as well as juvenile fish do not necessarily imply divergencies in reactive pattern. It may, rather, be a question of an identical reactional outfit answering with a varied behaviour to the different external conditions which face the members of the populations. In ethological, ecological and sociological work confusion easily arises if the concepts of habitat and habit are not treated with due regard to true causal interrelations between the organism studied and its surroundings. Modern work in these fields shows a most reassuring neglect of the old but surviving anthropocentric way of thinking, and considers instead the viewpoint of the organism studied.

Thus, to conclude, *C. lavaretus* and *C. nasus* presenting so obvious divergencies in habitat and habits differ, with certainty, only in one respect studied here, the gillrakers. Further studies, more thorough or extended to other qualities, may be able to furnish more conclusive information.

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Summary

I. By means of gillrakers countings in more than 1,300 specimens the *Coregonus* populations of the Sundsvall bay district in Sweden have been divided into two groups. The number of gillrakers proved in a rearing experiment to be unmodified. It is thought to be genetically fixed and the two groups are, according to SVÄRDSON, ranked as species, *C. lavaretus* L. and *C. nasus* PALLAS. Both species inhabit the coast. *C. lavaretus* spawns in the large rivers, *C. nasus* by the coast.

II. Movements have been studied by the tagging of 1,300 adult fish, with a return of 29 p.c. *C. lavaretus,* after spawning in the river, disperse along the coast mainly to the south. The maximum distance recorded was over 200 km. In midsummer the spawning migration sets in, probably all fish gathering every year in the home river. *C. nasus* populations along the coast are comparatively stationary, the populations of the species spawning close to the river mouth exhibit intermediate migratory habits.

III. *C. lavaretus* spawns later than does *C. nasus.*

IV. The offspring of the river spawning *C. lavaretus* leaves the river as eggs, fry and young (up to about 3 months old) probably in all cases passively migrating with the current. Such juvenile fish as are later found in the river, originate almost exclusively from whitefish populations in reservoirs and lakes upstream of that part of river accessible from the sea. The investigations have also been concerned with swimming speed and phototactic reactions in fry, and with growth and food in the young.

V. Evidence is lacking as regards the genetical nature of the differences studied here in the habits of the two species: in migration, spawning and biology of the young. They may all be created by external influences.

References

BERG, M. 1953. A relict salmon, *Salmo salar* L, called »småblank» from the river Namsen, North-Tröndelag. *Acta Borealia A 6: 1—17.*

CARLIN, B. 1955. Tagging of salmon smolts in the river Lagan. *Rept. Inst. Freshw. Res. Drottningholm, 36: 57—74.*

DAHR, E. 1947. Biologiska studier över siken, *Coregonus lavaretus* L, vid mellansvenska Östersjökusten. *Unders.-anst. sötv.-fisket, Drottningholm, Meddel. 28: 1—79.* (English summary.)

EKMAN, S. 1922. Djurvärldens utbredningshistoria på skandinaviska halvön. Stockholm 614 pp.

ELSTER, H. J. 1934. Beiträge zur Biologie des Blaufelchen. *Int. Rev. Hydrobiol. 30: 181—246.*

ESCHMEYER, P. H. 1955. The Pygmy Whitefish. *Coregonus coulteri,* in Lake Superior. *Trans. Amer. Fish. Soc. 84: 161—199.*

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

— and A. LINDROTH, 1954. Experimental observations on the spawning of whitefish. *Ibid. 35: 105—112.*

FREIDENFELT, T. 1933. Untersuchungen über die Coregonen des Wenersees. *Int. Rev. Hydrobiol. 30: 49—163.*

GRAY, J. 1928. The growth of fish III. *Brit. J. exp. Biol. 6: 125—130.*

HAYES, F. R. 1942. The hatching mechanism of salmon eggs. *J. exp. Zool. 89: 357—373.*

HOAR, W. S. 1953. Control and timing of fish migration. *Biol. Rev. 28: 437—452.*

JOHANSSON, B. 1956 a. Rommängd och romsvällning hos Indalsälvens sik. *Sv. Fiskeri Tidskr. 65: 144—145.*

— 1956 b. Fiskeförsök i Indalsälvens mynning 1954 och 1955. *Vandringsfiskutredn. Stockholm, Meddel. 7: 1—9.* (Typewritten.)

JÄRVI, T. H. 1934. Die Seefischerei von Finnland. *Handb. Seefisch. Nordeur. 8 (4): 1—72.*

— 1940. Über den Maränenbestand im Pyhäjärvi. *Acta Zool. Fenn. 28: 1—86.*

KENNEDY, W. A. 1954. Tagging returns, age studies and fluctuations in abundance of lake Winnipeg whitefish 1931—1951. *J. Fish. Res. Bd Canada 11 (3): 284—309.*

LAAKSO, M. 1951. Food habits of the Yellowstone whitefish *Prosopium williamsoni cismontanus* (JORDAN). *Trans. Amer. Fish. Soc. 80: 99—109.*

LINDROTH, A. 1942. Sauerstoffverbrauch der Fische II. *Z. vergl. Physiol. 29: 583—594.*

— 1946 a. Zur Biologie der Befruchtung und Entwicklung beim Hecht. *Unders.-Anst. sötv.-fisket. Drottningholm, Meddel. 24: 1—173.*

— 1946 b. Time of activity of fresh water fish spermatozoa. *Zool. Bidr., Uppsala 25: 165—168.*

— 1952. Salmon tagging experiments in Sundsvall Bay of the Baltic. *Rept. Inst. Freshw. Res. Drottningholm, 33: 57—69.*

— 1953 a, b. Sundsvallsbuktens hydrografi I and II. *Vandringsfiskutredn. Stockholm, Meddel. 10: 1—5; 27: 1—8.* (Typewritten.)

— 1953 c, 1954 a, Fiskeförsök i Indalsälvens mynning 1952 and 1953. *Ibid. 6: 1—5, 8: 1—6.* (Typewritten.)

— 1954 b. A stream tank at the Hölle laboratory. *Rept. Inst. Freshw. Res. Drottningholm, 35: 113—117.*

— 1955. Distribution, territorial behaviour and movements of sea trout fry in the river Indalsälven. *Ibid. 36: 104—119.*

LINDSTRÖM, TH. 1955. En undersökning av sikungar i Arjeplogsjöarna. *Sv. Fiskeri Tidskr. 64: 25—28.*

MASSMAN, W. H. 1952. Characteristics of spawning areas of shad, *Alosa sapidissima* (WILSON) in some Virginian streams. *Trans. Amer. Fish. Soc. 81: 78—93.*

MELLEN, IDA. 1923. The whitefishes (*Coregonus clupeaformis*) reared in the New York Aquarium. *Zoologica 2: 375—379.*

MONTÉN, E. 1948. Sikromstudier vid sjön Allgunnen N om Aneboda 1947. *S. Sv. Fiskerifören., Skr. 1947 (2): 33—46.*

MÜLLER, K. 1954. Investigations on the organic drift in north Swedish streams. *Rept. Inst. Freshw. Res. Drottningholm, 35: 133—148.*

NÜSSLIN, O. 1908. Die Larven der Gattung *Coregonus,* ihre Beziehung zur Biologie und ihre Systematische Bedeutung. *Verh. D. Zool. Ges. 18: 172—194.*

OLOFSSON, O. 1933. Rommängd och romsvällning hos siken. *Sv. Fiskeri Tidskr. 42: 277—279.*

— 1949. En sikromundersökning i Ringsjön. *S. Sv. Fiskerifören. Skr. 1948 (2): 75—77.*

OOSTEN, J. VAN, 1939. The age, growth, sexual maturity, and sex ratio of the common whitefish, *Coregonus clupeaformis* (MITCHILL), of lake Huron. *Mich. Acad. Sci., Pap. 24: 195—221.*

— and R. HILE, 1949. Age and growth of the lake whitefish *Coregonus clupeaformis* (MITCHILL), in lake Erie. *Amer. Fish. Soc., Trans. 77: 178—249.*

PRICE, J. W. 1940. Time-temperature relations in the incubation of the whitefish, *Coregonus clupeaformis* (MITCHILL). *J. gen. Physiol. 23: 449—468.*

ROSÉN, N. 1920. Om Norrbottens saltsjöområdes fiskar och fiske. *Lantbruksstyr., Meddel. 225: 1—94.*

RUSELL, E. S. 1937. Fish migrations. *Biol. Rev. 12: 320—337.*

SCHEURING, L. 1929, 1930. Die Wanderung der Fische. *Ergebn. Biol. 5: 406—691; 6: 4—304.*

SEGERSTRÅLE, C. 1947. Lake och sik som romtjuvar i österbottniska sikvatten. Fiskodling och fiskevård: 159—166. Helsingfors.

SLACK, H. D., 1955. Factors affecting the productivity of *Coregonus clupeoides* LACÉPÈDE in Loch Lomond. *Verh. Int. Ver. Limnol. 12: 183—186.*

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

— 1950. The Coregonid problem II. Morphology of two Coregonid species in different environment. *Ibid. 31: 151—162.*

— 1951. The Coregonid problem III. Whitefish from the Baltic, sucessfully introduced into fresh waters in the north of Sweden. *Ibid. 32: 79—125.*

— 1952. The Coregonid problem IV. The significance of scales and gillrakers. *Ibid. 33: 204—232.*

— 1953. The Coregonid problem V. Sympatric whitefish species of the lakes Idsjön, Storsjön and Hornavan. *Ibid. 34: 141—166.*

— 1955. Salmon stock fluctuations in the Baltic Sea. *Ibid. 36: 226—262.*

— 1957. Sikar och siklöjor, inte två men sju olika fiskar. *Sv. Fiskeri Tidskr. 66: 1—4.*

TALBOT, G. B. 1954. Factors associated with fluctuations in abundance of Hudson river shad. *U.S. Fish Wildlife Serv. Fish. Bull. 101: 372—413.*

THIENEMANN, A. 1915. Untersuchungen an Coregonen. *Z. Fischerei, NF 1 (314): 168—196.*

TOOTS, H. 1949 a. Maränenfischerei im Fluss Gimån (Jämtland). *Rept. Inst. Freshw. Res. Drottningholm, 29: 146—152.*

— 1949 b. En sikrompump. *Sv. Fiskeri Tidskr. 58: 97—98.*

— 1951. Number of eggs in different populations of whitefish. *Rept. Inst. Freshw. Res. Drottningholm, 32: 133—138.*

WAGLER, E. 1941. Coregonen. *Handb. Binnenfisch. Mitteleur. 3 (6): 371—501.*

VALLIN, S. 1936. Utplantering av gädd- och sikyngel i saltvatten. *Sv. Fiskeri Tidskr. 45: 124—127.*

Baltic Salmon Fluctuations: A Reply[1]

By Arne Lindroth

The large simultaneous fluctuations of the salmon catch in the Baltic Sea and its tributary streams, characterizing this confined area, have raised much interest. In Sweden surveys have been given by Alm (1924, 1934) and Lindroth (1950).

For my part I arrived at the preliminary conclusion that the main factors producing the large-scale fluctuations in the Baltic salmon stock must be sought in changes in the biological balance induced by climatic factors. Reference was made, *inter alia,* to the connection between severe winters and subsequent good salmon years and the possibility was mentioned that the common porpoise, which is sensitive to heavy freezing in the Baltic, could constitute the effective link in the causal chain.

I suggested also that the small-scale variations in the catch be studied as deviations from a "salmon curve" (a curve drawn freely and by hand summarizing and generalizing catch trends in the salmon rivers of northern Sweden) thus avoiding the influence of the predominant large-scale factor. Several factors possibly responsible for these yearly variations were listed with references to earlier authors. It was mentioned, *inter alia,* that fluctuations in the year-class composition of the running stock, caused by temperature conditions, must continually influence the catch curves of the rivers.

Recently, in this series of Reports, Svärdson (1955) has discussed these problems. His paper has prompted me to the following discussion.

Svärdson bases his comments mainly upon the work of Jurva (1952) on the ice-cover of the Baltic in a series of winters and, in addition to the salmon curve, on statistical information concerning the salmon catch at the Svartö weir in the river Lule älv.[2] He asserts a significant correlation between 3-years means for the extent of maximum ice cover and the numerical values for the salmon curve 5 years later giving several examples of rich salmon years (river catch) about 5 years after a severe winter. By means of statistical treatment of catch data from the Svartö weir he ascertains a mathematical correlation between mild winters and good catches the 3rd summer thereafter and between severe winters and good catches culminating in the 6th summer after the winter in question.

The main causes of large-scale fluctuations demonstrated in the salmon curve are, according to Svärdson, firstly the variations in the porpoise stock effected by very severe ice conditions and by porpoise hunting in the Danish

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[1] Report from The Migratory Fish Committee.

[2] For all place-names mentioned in this paper see Fig. 1.

sounds which are regularly passed by the porpoise migrating between the Kattegatt and the Baltic.

Responsible for the small-scale or yearly fluctuations are the accelerating or delaying effects of temperature upon the smolt migration from river to see and upong spawning migration from sea to river.

SVÄRDSON's conclusions, given in this general form, can be wholly or in part accepted and are, essentially, not new. His special discussions, however, cannot be accepted.

The material

1. *Ice and temperature conditions*

SVÄRDSON has based his studies on JURVA's estimate of maximum ice cover in the Baltic area 1830—1951. This material agrees with the Swedish figures used by myself (ÖSTMAN 1937) but is more detailed and covers a longer period. (In PALOSUO, 1953, ice values are given from 1720.) JURVA's figures also agree with the known temperature records from Stockholm (LILJEQUIST 1943, see PALOSUO 1953) used in the statistical calculations worked out for me by S. PERSSON (LINDROTH 1950).

The material mentioned is used by SVÄRDSON not only when studying phenomena for which the ice cover is possibly the effective factor but also as a measure of spring temperatures in the sea and in the river (cf. below).

2. *Catch data*

a. The salmon curve. This curve (drawn free hand) is only to be used when studying the large-scale fluctuations, as the yearly variations are totally smoothed.

b. The Svartö weir in the river Lule älv. OLOFSSON (1935), whose knowledge of the local conditions is outstanding, warns explicitly against using the data from individual weirs "as a basis for general conclusions regarding salmon abundance and salmon run in the whole" (my translation). According to SVÄRDSON the catch "probably can be regarded as being representative for the River Lule and the whole of the northern Baltic". The case can be mathematically studied. Table 1 demonstrates the catch relationship between the Svartö weir and the rivers Luleälv and Indalsälven. A highly significant correlation is seen to exist in the short period studied (31 years fit for use) as regards the catch at Svartö weir and the total catch in the river Luleälv. The same holds true also for the river Luleälv and Indalsälven during these years. For the Svartö weir *versus* Indalsälven the correlation is insignificant. The correlation between catches at the Svartö weir and Indalsälven turns out to be still more insignificant when the longer period, here applicable, is

Fig. 1. Map of the Baltic area with place-names mentioned in the text. 1. The Svartö weir. 2. The island Agö. 3. Middelfart. 4. Aerö.

considered. This is also the case when, in the computations for Svartö weir *versus* Luleälv, the few existing older values are added.

The above results are explained by the fact, obvious from Fig. 2, that the Svartö weir, as compared with the rivers discussed, underwent a serious decline at the turn of the century; perhaps the decline is continual. For

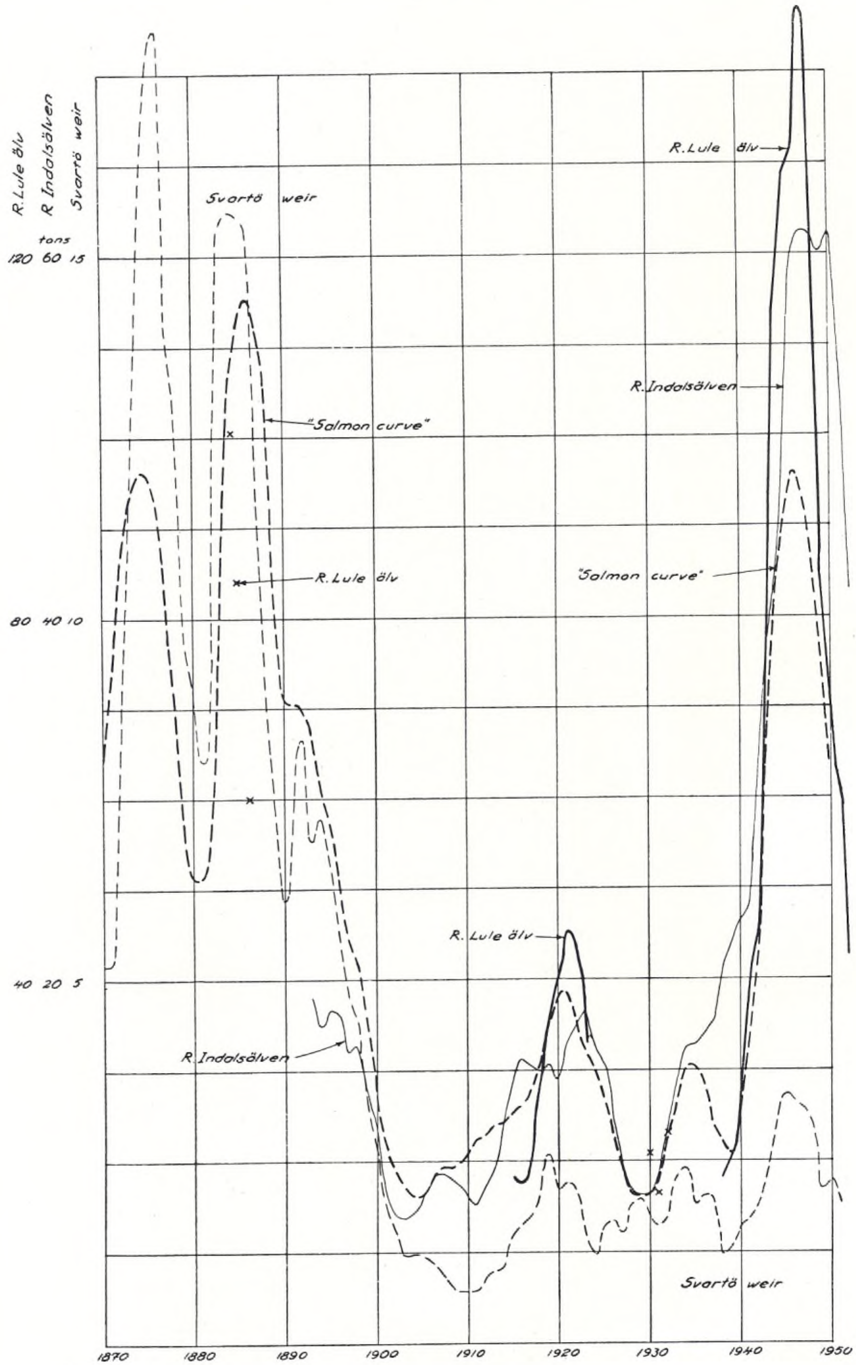

Fig. 2. The salmon curve and 5-year catch means for the rivers Lule älv and Indalsälven and for the Svartö weir in Lule älv. X=yearly catch figures for Lule älv.

Table 1. Correlation between river catches.

Catch places	Period	Pairs of variables	Correl. Coeff.	Probability
Lule älv—Svartöfisket	1914—1951	31	0.74	< 0.001
Lule älv—Svartöfisket	1884—1886 1914—1951	34	0.34	0.05—0.10
Indalsälven—Svartöfisket	1914—1951	31	0.36	0.05—0.10
Indalsälven—Svartöfisket	1892—1951	60	0.19	0.10—0.20
Lule älv—Indalsälven	1914—1951	31	0.73	< 0.001

shorter periods the correlation is mathematically good but not for longer periods. The outstanding series of catch records for the Svartö weir is, therefore, not to be regarded as representative even for the local river in studies comprising a long period or uncorrected catch data.

Statistical treatment of data

1. The relationship between 3-year means for ice cover values and salmon curve figures 5 years later has been studied by SVÄRDSON who finds the correlation coefficient 0.3405 with a level of significance of 0.002.

Correlations and significances for, on the one hand, 3- and 5-year ice value means (the latter are to be preferred as the salmon curve bases upon 5-year means) each paired in 9 different series with, on the other hand, salmon curve figures 1 year before to 7 years after the ice figures, are computed in Table 2. The correlation is not intimate but the level of significance is high troughout. Our attention is commanded by the almost significant correlation between ice conditions and the salmon catch *one year before* and by the fact that in one series the leval of significance is somewhat higher at 6 and 7 years displacement than at 5 years.

Table 2. Correlation between maximum Baltic ice cover and salmon catch in the rivers (salmon curve). 81 pairs of variables.

Catch year relative to ice year	3-year means for ice		5-year means for ice	
	Correl. coeff.	Probability	Correl. coeff.	Probability
—1	0.22	0.02 —0.05	0.24	0.02 —0.05
0	0.19	0.05 —0.10	0.23	0.02 —0.05
1	0.18	0.10 —0.20	0.26	0.02 —0.05
2	0.20	0.05 —0.10	0.29	0.001—0.01
3	0.23	0.02 —0.05	0.34	0.001—0.01
4	0.27	0.01 —0.02	0.39	< 0.001
5	0.29	0.001—0.01	0.42	< 0.001
6	0.31	0.001—0.01	0.42	< 0.001
7	0.30	0.001—0.01	0.38	< 0.001

Table 3. Correlation between maximum ice cover and salmon catch (salmon curve) in A. the high- (1870—1900) and B. the low-catch period (1901—1950) at 5 years displacement.

Period	Pairs of variables	3-year means for ice		5-year means for ice	
		Correl. coeff.	Probability	Correl. coeff.	Probability
A	31	—0.05	0.7 —0.8	—0.07	0.7 —0.8
B	50	0.23	0.1 —0.2	0.40	0.001—0.1
A + B	81	0.29	0.001—0.01	0.42	< 0.001

Evidently there exists a mathematical correlation between ice cover in the Baltic and the salmon catch.

Wether Svärdson intended to stress only this fact is not quite clear; his solitary reference to the 5-year displacement suggests a belief that this very displacement is responsible for the significance arrived at and that the method rendered possible a study of yearly variations (among which the 5-year displacement receives his special interest, see below). However, this value must be compared with computations of other possible displacement and these (Table 2) prove that the placing of any particular stress on the 5-year displacement is unjustified.

If the material available is divided, as is appropriate, into one period of good catches and one other of bad catches, the limit being arbitrarily placed at the turn of the century, values for correlation and significance may be read off from Table 3. The former period demonstrates no correlation whatsoever between ice conditions and catch 5 years later. The latter period (comprising shorter periods of good catches) demonstrates an almost significant or significant correlation.

If, furthermore, 1900 is taken as the last year in a longer period of recorded winters we find the distribution of winters over catch periods given in Table 4, the winters classified after Svärdson as strong, medium or mild according to the extent of ice cover.

We come to the conclusion (indicated already by graphical plotting of the data) that a statistically certified relationship exist between extent of ice cover in the Baltic area and the salmon catch in its rivers in so far as periods distinguished by very extensive freezing are accompanied by good salmon catches whereas periods of milder winters (or periods devoid of very severe winters) are accompanied by inferior catches. A study of the catch peaks in this century reveals moreover, as exemplified by Svärdson, that these peaks follow some years after the severe winters. Any connections of wider application regarding the yearly variations cannot be studied in the material hitherto handled which is to a predominating degree influenced by the alternation between periods of high and low catches.

Table 4. Distribution of winter classes (Nr. per 10 years) over high- (1830—1900) and low-catch period (1901—1951).

Winter class	Strong	Medium	Mild	Sum
High-catch period	3.9	2.3	3.8	10.0
Low-catch period	2.0	3.8	4.2	10.0

2. SVÄRDSON also computed the mean catches in the Svartö weir 1 to 6 years after the winters grouped into the above-mentioned three classes.

The value of the Svartö weir data as a basis for statistical treatment is discussed above. Leaving its imperfections aside, we find that, in most cases, every displacement studied after strong winters shows a catch mean above the common mean. This is, however, nothing but the expected consequence of the mathematically demonstrated fact that good catches are concentrated to periods of strong winters. High levels of significance are natural.

Medium winters are regularly accompanied by catch means below the over-all mean value (not by average catches as stated by SVÄRDSON; in that case the total catch would consist of mean catches plus good catches which is preposterous). The explanation is the same: the medium winters are concentrated in the period of low catches. Furthermore, the Svartö weir catches in particular show an abnormally great difference between the high and low catch periods, rendering it unrepresentative, as pointed out above.

The mild winters, fairly evenly distributed over the two catch periods chosen, are, consequently, accompanied by, on an average, mean catches — with a maximum, however, for the 2-year displacement (when the mean catches for strong winters are at the total mean level). The probability for this case is given as 0.04.

The study of interrelations between a certain factor and its supposed result, *e.g.* the catch a certain number of years later, by means of the computation of correlations, requires that the dependant variables used are devoid of direct or indirect connections except the one studied. This condition is not fulfilled in the computations under consideration here. Apart from the fact that one and the same year-class of salmon contributes to the catch in consecutive years (thus constituting a possible direct connection between years) we have to consider the circumstance that the catch periods are, to a certain degree, dependant upon a long-term fluctuation and the individual catch values for, *e.g.,* the low-catch period weigh considerably less in the mean value computations, than the higher catches of the high-catch period. The correlations and significances arrived at cannot be supposed to reveal true biological interrelations of the nature presumed, *i.e.* between separate years.

If a division into high and low catch periods is undertaken also in the case

Table 5. Mean catches (in tons) in the Svartö weir in high- and low-catch periods distributed over mild (—), medium (0) and strong (+) winters, 0 to 6 years before the catch years.

Ice year relative to catch year	High-catch period 1835—1900			Low-catch period 1901—1951			Sum 1835—1951			after Svärdson[1]		
	—	0	+	—	0	+	—	0	+	—	0	+
0	9.9	8.6	9.9	1.9	1.7	1.5	6.2	4.7	7.7	—	—	—
—1	9.3	9.2	10.3	1.8	1.6	2.0	6.0	5.0	7.7	6.5	5.6	7.8
—2	11.8	8.1	8.3	1.8	1.8	1.6	7.6	4.5	6.2	8.3	4.6	6.5
—3	11.2	6.5	9.8	1.7	1.6	2.1	7.0	3.8	7.4	7.4	3.9	7.7
—4	9.0	10.0	9.9	1.5	1.5	2.7	5.7	5.2	7.7	5.7	5.2	8.3
—5	8.7	9.3	10.6	1.7	1.6	2.2	5.7	4.8	8.2	5.7	4.8	8.5
—6	8.9	9.6	10.2	1.8	1.5	2.3	5.8	4.7	8.1	5.8	4.7	7.9

[1] Computations not wholly comparable.

of the Svartö data, the values demonstrated in Table 5 are found. Firstly it may be stated that the material when undivided corresponds quite well with the values presented by Svärdson, although the method of calculation is somewhat different. After division, however, the trends differ. Treating the data, we see how a few high chatches influence the various means: *e.g.* certain very high catches 2 years after mild winters, and the catch peak in the 40s causing high figures for the 4-, 6-, and 5-year displacements after the strong winters 1940—1942 in the order mentioned. The conclusions which it was possible to express after the superficial examination of the undivided material, do not gain support after this division has been made. For the low catch period, it cannot be stated that the catch "after a mild winter . . . increases, culminating in the third summer". Catches correlated with severe winters dominate in only 3 (4) cases of displacement out of 7 in the high-catch period and in the low catch period (with a more pronounced dominance) the maximum lies at 4 years displacement; the conclusion that »after a severe winter the salmon yield increases significantly, culminating in the sixth summer" is not justified.

A more thorough mathematical examination of the treatment of the Svartö data would in all probability make it clear that, even in this case, the long-term catch fluctuations and the distribution of the winters over catch periods are responsible for the results. It is not permissible, in this case either, to interpret the results as general correlations between yearly variations. And it ought to have awaken suspicion when the calculations in the one case (using the salmon curve) resulted in apparently significant correlations on the basis of a rectilinear relationship (implying the lowest catches after the mildest winters) whereas, in the other case, the Svartö data calculations are founded upon a curvilinear relationship (implying, *e.g.*, that mild winters give higher catches than medium winters).

3. In my opinion we have to deal with a typical case of "mixed connections of covariances" (BONNIER-TEDIN 1940, my translation). In fact, agreement seems to exist concerning the main point, that is, the existence of a least three different connections between temperature conditions and salmon catch.

It is probable that we have one primary fluctuation giving periods of several years, varying in length and frequency, upon which are superimposed many secondary fluctuations of different origin, frequency and length down to the yearly variations (cf. LINDROTH 1950 Fig. D 9). These smaller secondary fluctuations cannot be mathematically treated without due regard to the dominating primary fluctuation. SVÄRDSON has neglected this and on the basis of direct computations on the uncorrected data, has drawn conclusions concerning primary as well as secondary fluctuations. A certain value for, say, high salmon catch serves, therefore, in this case in three different computations and is allotted as many quite different causes.[3] The misinterpretations made have, when faced with biological reality, led to considerable difficulties and efforts to bring the statistical results into agreement with biological facts have been unsuccessful.

The primary fluctuation

The mathematical treatment of data has confirmed the general impression that a strong connection exists between ice conditions in the Baltic area and the river salmon catch.

The nature of this connection is not clear, not even wether it is a case of cause and effect or not. The current discussions centre upon a predator: prey relationship. During river life, at least in the northern rivers, certainly mergansers (LINDROTH 1955), probably freshwater sculpin (cf. *e.g.* SHAPOVALOV and TAFT 1954) and burbot, but scarcely grayling[4] are of great importance. In the sea the river lamprey is very suspect (investigations are in progress). Fluctuations in the population density of these animals and

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[3] The three cases may be summarized thus: 1. extensive ice cover — porpoise mortality — abundant salmon populations, 2. small ice cover — high temperature in the sea — many salmon deciding to spawn in the second year thereafter, 3. extensive ice cover — low river temperature — accumulated smolt migration the next year — peak run the fifth year. The cases are dealt with below.

[4] According to SVÄRDSON "it seems probable that the grayling is *the most serious* natural fry predator" (1955, my italics). No evidence is produced for this statement. The observations of TRYBOM (1908) referred to, concern salmon eggs taken by graylings — most probably these eggs had got outside the redds or been dug out by repeated spawning in occupied nests and were in any case lost. TRYBOM states explicitely that parr of salmon or sea trout were not found in the grayling whereas it had preyed upon other fishes in 29 of 257 cases (October—December). 141 graylings caught in the river Indalsälven (July—August 1952) contained fish diet only in three cases: 3 to 4 years old fish with 1, 2, and 3 sculpins in each (personal communication H. PETERSON).

of the seal species are likely to influence the salmon population. **Svärdson** is of the opinion that the main factor lies in the sea and attributes it to the common porpoise (*Phocaena phocaena*). I still believe this to be one plausible link in the causal chain. Several points need, however, elucidation.

As pointed out by **Svärdson** it is to be assumed that the porpoise is bound to take very small salmon during its first season in the sea. Unpublished Danish investigations demonstrate the absence of prey larger than about 30 cm although larger-sized fish (cod) ought to have been available (**Möhl-Hansen** 1956, personal communication; no salmon was found in the stomachs of the porpoises but was not to be expected in this material either). It must be stressed, however, that any conclusive evidence of the salmon as a major constituent in the food of the porpoise is still missing.[5]

Should a porpoise feed exclusively on salmon weighing about 150 g, *i.e.* about 25 cm, for 200 days of the year, this porpoise, at an arbitrary food requirement of say 5 kg per day for a 60 kg porpoise,[6] would consume some 7,000 young salmon per year. This figure is to be compared with the total smolt number which has recently been estimated to be in the value of 4,000,000 as a yearly mean produced by the larger North Swedish rivers (**Lindroth** 1957). The figure given denote the *possible* importance of the porpoise as influencing the salmon population.

Porpoise mortality effected by extensive freezing of the Baltic is shown by numerous field observations. Besides records referred to by **Svärdson** (whose qoutation of Johansen, 1929, is in part incorrect), **Johansen**'s report (1929) on many porpoises stranded in the Sound during a severe winter in the 1870s is worth recalling. A porpoise kill in 1947 at Aerö may also be mentioned (J. **Thiessen**, Teglgaard, Middelfart, personal communication).

The Baltic porpoise population is known to have been almost exterminated during the severe winters 1940—1942.[7] If a large share of the sea mortality of the salmon is to be charged upon the porpoise, the heavy reduction of the porpoise in 1940—1942 ought to have resulted in a simultaneous large in-

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[5] According to **Tauber** (1892) the porpoise at Bornholm in the southern Baltic preys "perhaps mainly upon salmon" (my translation). Real evidence of the porpoise taking salmon in the sea seems to be very scanty. **Macintyre** (1934) says: "It has been suggested that the porpoise does not interfere with salmon but I *once* saw a large one chase a salmon into shallow water, where it sought shelter under a stone, and its pursuer turned off to sea. . . . A herring fisher*man* . . . assured me that he had seen *a* porpoise chase and capture a salmon, . . ." (My italics.) Compare **Svärdson** (1955): "It has been argued that the porpoise probably does not catch salmon. **Macintyre** (1934) observed porpoi*ses* chasing salmon and reports fisher*men's* observati*ons* according to which porpoises may catch salmon in the open sea." (My italics.)

[6] *Tursiops truncatus* in captivity is said to require 15 pounds per day for a 2 m whale (about 100 kg). (K. **Curry-Lindahl**, personal communication.)

[7] Whereas shoals of porpoises are said earlier to have been a common sight along the coasts of the county of Västernorrland (off the rivers Ångermanälven to Ljungan) only a few have been seen since the winters 1940—1942 according to the local fishermen.

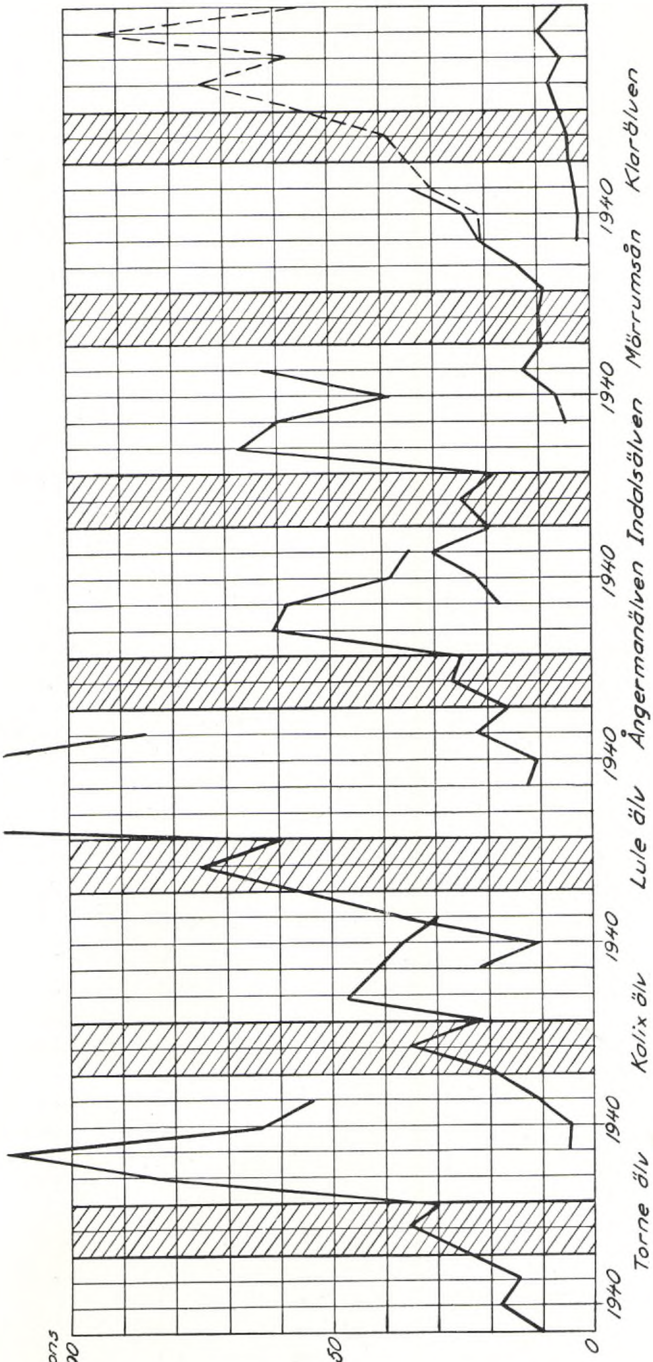

Fig. 3. Yearly catch figures for some rivers around the years 1942—1944 (shaded) according to the official records. The broken line for the river Klarälven=decitons.

crease in the salmon catch in all Baltic rivers beginning with small salmon (2 years at sea) 1942—1944 followed by ordinary salmon one year later. In Fig. 3 some relevant catch data are compiled. The increase in the years mentioned is moderate. For Indalsälven and Ångermanälven the increase is doubtful not to mention Mörrumsån. On the other hand, Klarälven, whose landlocked salmon population is in no way connected with the Baltic salmon stock, or with porpoises, takes part in the general trend. Throughout, the rise is more marked *after* the expected years, a fact which can be explained only to a limited extent by delayed exploitation. The whole case is without doubt worth a detailed study and cannot, thus, be regarded as solved. The exact time for the general catch increase seems, superficially judged, in better accordance with some influence in the rivers, expressed in the catch 5—6 years later.

As a new contribution to the discussion SVÄRDSON introduces the porpoise hunting in the Danish sounds, a very attractive idea. As regards the number of porpoises killed his only source of information seems to be EKMAN's revision of BREHM's "Tierleben" (1938) according to which the mean yearly yield in Gamborg fjord close to Middelfart amounted to 1,000 to 2,000 animals with a record figure of 3,000.

The porpoise hunting in Gamborg fjord has been carried on from early times up to 1892 inclusive and later, during the two world wars, 1916—1919 and 1941—1944 (as also stated by SVÄRDSON). The yield figures mentioned above refer to the 19th century and earlier. For the period 1916—1919 I have obtained some imprecise verbal information from a former hunting foreman (J. THIESSEN). For the last period the total catch of three seasons (or what was almost the total catch) is comprised in the collection of 695 animals treated by MÖHL-HANSEN (1954; personal communication 1956). All available records have been collected in Table 6. The figures are on an average not so high as indicated by EKMAN's statements. It this connection it is to be noted, however, that in older times porpoise hunting was carried on in more places than in Gamborg fjord (IRMINGER 1846, TAUBER 1892).

It is possible to obtain information about the effect of the porpoise hunting in two ways 1. by studying directly the porpoise population or, provided a causal connection between porpoise and salmon exists, indirectly, by studying the salmon, 2. by estimating the relative number of porpoises killed.

The first of the possibilities mentioned is infortunately out of the question as for the last say 80 years (when observations on porpoise frequency would be remembered and applicable salmon catch records are available)[8] the

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[8] Recently BERG (1957) has been able for some of the salmon rivers to extend a salmon curve to as far back as 1800. His data compared with PALOSUO's and JURVA's ice values furnish more material for this discussion. I will, however, confine myself to pointing out the low catch values around 1810 which superficially coincide with a pause in the

Table 6. Porpoises caught in Gamborg fjord.

Year	Nr.	Comments
1770 s	100—125	"earlier" 500—700 per year (Behrendt 1929)
1800—1819	Stoppage	1819—1892 regular hunting (Behrendt 1929)
1834/35	1684	
1835/36	1215	
1836/37	1416	
1837/38	653	
1838/39	886	
1839/40	657	Irminger 1846
1840/41	683	
1841/42	793	
1842/43	1395	
1843/44	1079	
1844/45	330	early and prolonged winter
mean	980	
1880/81	1831	
1881/82	1814	
1882/83	1545	
1883/84	1505	
1884/85	1552	
1885/86	1318	Behrendt 1929
1886/87	1349	
1887/88	1009	
1888/89	1389 + 200	
1889/90	692 + 300	
1890/91	198 + 103	"Marsvinslauget" dissolved, the hunting ceases,
1891/92	497 + 28	partly economical causes
mean	1278	
1916	200—300	
1917	200—300	Verbal estimation by J. Thiessen
1918	500	All exported to Germany
1919	700	
mean	425	
1941/42	700	
1942/43		
1943/44		
mean	233	
mean 1834—1944	951	

porpoise hunting has been fairly coincident with severe winters sometimes accompanied by observed porpoise winter kill (1870s, 1940—1942) sometimes not so (1916—1917). Observed winter kill of porpoises without hunting exists, on the other hand, in some cases (1924, 1929, 1947).

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porpoise hunting 1800—1819 (see Table 6). The catch values for the rivers in question seem however to rise before 1819 and the rise may just as well be connected with the severe winters in 1809 and 1814. (The catch records from the Svartö weir indicate a peak during the pause or 1808—1809.)

We know that the female porpoise bears but one young every year, when fertile (MÖHL-HANSEN 1954), but information is lacking as regards the span of life of the female and, consequently, number of young produced per female. Nor do we know the size of the Baltic porpoise population. In these circumstances it is in my opinion precocious to assume that the number of porpoises killed by hunting makes a considerable rate of mortality in the stock (SVÄRDSON).

Information from two of the porpoise hunting foremen of the last hunting periods (J. THIESSEN and J. HANSEN, Middelfart) seem to indicate that only a small fraction of the migrating porpoises were killed at Middelfart. In December and January "thousands" travelled past day and night. Hunting was performed on an average 5 days per week with at most 8 beatings per day. At every beating a certain flock was aimed at and meanwhile other flocks escaped through the sound.

This information concerns the two hunting periods in this century. During the latter period the hunting was impeded by mine-sweeping and ice — its lack of success cannot, therefore, be taken as indicative of a population diminished by the foregoing three very severe winters.

The circumstances mentioned here give no support to the opinion that porpoise hunting is of any great importance for the porpoise population. Moreover the sound past Middelfart constitutes but one of the three connections between the Baltic and the Kattegatt. The earlier porpoise hunting on other places has been of still less importance.

In my opinion it is premature to take for granted any considerable effect of hunting on the porpoise population and a very expensive experiment to reduce the population by revived hunting, suggested by SVÄRDSON, ought to await general studies on the porpoise in the Baltic and special investigations on the food of this whale.

Secondary fluctuations

SVÄRDSON interpretes the result of the mathematical treatment to the effect that the 3rd summer (2nd year) after a winter with slight ice cover and the 6th summer (5th year) after a winter with extensive ice cover should give rich river catches. (See above.)

The effect of a mild winter

SVÄRDSON sums up that the correlation between slight ice cover (which in turn is supposed to be correlated with relatively high spring temperatures in the sea)[9] and the subsequent increase in salmon catches during "the next few years is probably due to the effect of high sea temperatures in spring on salmon run". We should therefore expect this effect to be evident during the catch season following the warm winter (*i.e.* the high spring sea temperature) as demonstrated by JACOBSEN and JOHANSEN (1921) for Gudenaa, ALM (1924) for Mörrumsån and as we may understand also from SVÄRDSON (pp. 238, 239, 245). His mathematical treatment of the connection between winters and subsequent catches lacks, however, this very comparison. When it is computed (see Table 5), the mean catches in the combined material turn out to be greater in the summers after *strong* winters than in those following mild winters (in the divided treatment the results differ). For one who accepts the validity of the statistical method this does not agree. SVÄRDSON seems then to mean that a warm spring speeds up the growth of salmon whereby they "become capable of running in the next few years". An argument biologically closer at hand would be to stress the increased run in or immediately after warm seasons (amply quoted by SVÄRDSON) which would come the remaining sea stock to decrease giving *bad* catches in the years to follow. Or, why not (agreeing with SVÄRDSON, see under the following head): a mild winter is correlated to warmer river water in spring and, thereby, induces many smolt to migrate giving good catches of small salmon two years later. This would even agree with the statistical result but not with SVÄRDSON's argument under the following head, according to which increased smolt migration gives good catches *four* years later (see below). (In my opinion this interpretation fails by the lack of correlation between ice values and river temperatures.)

While discussing this subject SVÄRDSON also touches upon the influence of river temperature upon the run and it is probable that his adoption of a delayed catch increase after mild winters is connected with his assumption that salmon does not run when the river water is colder than the sea water. From a misinterpreted graph on water temperature in the river Ljusnan 1913—1924 compared with sea surface temperature at Agö 1931—1938 (the monthly means stand wrongly for the first day of the month) he concludes that "homothermy" is attained "about August 1st or a few days later" (to date such an event so exactly is not, of course, justified) and that "after that date, no more runs seem to occur in Swedish rivers". No evidence or references are given for this hypothesis. Investigations exist. NORDQVIST (1924) points out that salmon run at almost every time of the year and considers the water temperature to be devoid of regulating influence (whereas extreme cold could act as a stop). Late autumn runs of atlantic salmon are

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[9] This is probable. Correlation computations of the rich data from Swedish lightships have yielded significant correlations for May and, partly, June. It is however to be noted that the salmon is likely to some extent to choose its water layer and, consequently, water temperature.

common in Canadian rivers where the late-running fish may remain in the coastal waters, not entering the river until spawning time (**Belding** and **Kitson** 1934).[10] And in spite of three years daily contact with the salmon fishery in river Indalsälven I cannot verify the opinion that the run should be at an end on August 1st or, if the graph is correctly interpreted, on August 15th. The climax has passed, that is true.

In short, it seems impossible to assume an effect of little ice in the Baltic, causing, in the way suggested by **Svärdson**, through all the influences of two intervening years, an increase in salmon run the 3rd summer thereafter. And yet, this is demanded by the interpretation of the statistical results. The interpretation is, in my opinion, devoid of any biological foundation.

The effect of a severe winter

Svärdson points out that the smolt transformation is reported to be influenced by temperature, in a warm spring many smolt migrate who, had the spring been cold, would have remained in the river one more year. Such a behaviour seems very plausible.

The extent of ice cover in the Baltic is apparently assumed to be correlated with the water temperatures of the rivers in spring. Table 7 shows a control of this tacitly made postulate for the river Indalsälven. For the month of April there exists an insignificant negative correlation, for May a correlation which is on the point of being almost significant and for June an insignificant negative correlation. An evaluation of Baltic ice conditions is apparently no useful substitute for spring water temperatures of the rivers. (Note that the smolt migration of the main Baltic rivers occurs about June.)

However, extended ice cover in the Baltic should be correlated with cold river water and this should, in turn, bring about a postponement of the smolt transformation causing an increase in the number of migrating smolt the following year an effect which could be accentuated if this spring was warm. The latter connections are *per se* very plausible.[11] On the other hand it is not plausible when **Svärdson** adopts the hypothesis that a cold spring could delay the smolt migration to the late summer — so late that the sea has become warmer than the river (a fact not perceived by the smolt until already out of the river mouth). This explanation of a postponed migration has no support. Existing facts all indicate that the smolt leave the rivers of

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[10] **Belding** and **Kitson** (1934) are of the opinion that "the high temperature of the southwest Margaree is apparently the factor which limits the run in this branch to early spring and late fall, . . .»

[11] It is to be observed that of the equally probable causes for many smolt migrating (a *cold* spring the year before and a *warm* spring the actual year) only the former has found expression in the statistical result and the whole phenomenon is discussed under the heading "The delaying effect of a severe winter".

Table 7. Correlation between ice cover in the Baltic and river water temperatures in Indalsälven 1909—1948.

Month	April	May	June
Pairs of variables ...	16	30	39
Corr. coeff.	– 0.16	—0.36	—0.09
Probability..............	0.5—0.6	0.05—0.10	0.5—0.6

northern Sweden in June, possibly also around the beginning of July (own observations in the Indalsälven, Gide älv after ÖQUIST, Lule älv after ENEQUIST, personal communications). Autumn migration, discussed in some cases (see *e.g.* SCHEURING 1939) is not probable.

But let us keep to the case of a smolt migration postponed for one year after a severe winter. The fish return partly as grilse (which in some years may be far more common than indicated by the catch records) partly as small or larger salmon. If then "they arrive at the home river before homothermy between river and sea in August, they rise in the same season, if not they must *probably wait by the shore* until next spring" (my italics). No evidence is given for this assumption. In this way, however, a distribution of the running salmon over the 4th, 5th, and 6th summers after the cold winter with a statistical significant correlation for the 6th summer would be explained. The salmon in that case would have been, most of them, 4 years at sea. This age is commonly supposed to be attained by only a few salmon [12] — great numbers of such an age group would considerably increase the individual mean weight. Moreover the delayed and consequently older smolt tend to give a shorter sea life (see *e.g.* SVÄRDSON).

Finally, if such a smolt year-class, enlarged on account of temperature conditions, returns to the rivers affecting on an average mainly the catch (in bulk) 4 years later, this ought logically to be true for *all* smolt year-classes and the river catches would, consequently, depend on the whole upon fish with 4 sea years. Which is not, however, the case (see footnote 12).

With the aid of a series of largely unverified or unlikely conjectures SVÄRDSON tries to give a biological explanation of his mathematical connection between severe ice conditions in the Baltic and good salmon catches the 6th summer (5th year) thereafter. The bulk of adult salmon in these year-classes are by then dead. They would be even more so if we, from the mathematical correlation between severe freezing and the salmon curve figures 6 or 7 years later (see Table 2), vindicated an analogous explanation of this correlation.

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[12] According to ALM (1934) 7.6 p.c. of maiden salmon have 4 years at sea, the figure decreasing to about 3 p.c. if only salmon with comparatively higher smolt age are considered as applicable in this case.

Discussion

We must avoid any explanation of the computed correlations between Baltic ice conditions and salmon catch which implies any connections between individual years. In my opinion, expressed earlier (1950), the studies of yearly fluctuations ought to be directed upon the *deviations* from the actual catch level (given *e.g.* as mean catch for a suitable number of years) and upon the interconnections of such deviations (as between rivers) and their connections with measurable factors supposed to affect organisms: food, predators, diseases and hydrological conditions. Success is hardly to be expected from a concentration upon any single factor: temperature (or, to be correct, Baltic ice conditions, as SVÄRDSON) or river water levels (as HAGMAN 1938, see LINDROTH 1950).

Furthermore, our material should when this is feasible measure the actual factors. Concerning sea and river water temperatures an abundance of data is available and of course is far preferable in this case to supposed or mathematically more or less significant correlations with ice cover in the Baltic.

Results of such studies are available as illustrated by the following examples.

1. The connection between sum of river water temperature June—September for three consecutive years and the river age of smolt hatched in the spring of the first year. (Torne älv, for material see LINDROTH 1950.) For 12 pairs of variables an almost significant correlation coefficient of 0.69 is obtained (P-value 0.01—0.02). The biologically very plausible event, indicated by SVÄRDSON *inter alios, i.e.* that the water temperature affects the growth of parr and consequently the mean river age, receives thus a certain statistical support.

SVÄRDSON seems inclined partly to connect the smolt age with the temperature, or with temperature gradients, as stimuli for the smolt transformation which is of course plausible and open to closer study.

2. The connections between percentage deviations from 5-year catch means in the rivers Lule älv and Indalsälven. For 26 applicable pairs of variables the almost significant coefficient of correlation 0.45 is obtained (P=0.02—0.05). In 15 cases out of 23 these relative catch figures show simultaneous increase or decrease, in the 8 remaining cases the value rises in one river and falls in the other. (For the absolute catch values the corresponding figures are 17 to 8, out of 25.)

The question of the conformity between the yearly catch fluctuations in the different salmon rivers is of primary interest and the solution of this question must take precedence over every attempt to connect these fluctuations with common factors. Should a strong connection be proved it is probable that the yearly fluctuations are ruled by general factors in the rivers, or in groups of rivers, or in the sea — should however the connection prove to be weak or absent the working factors must be local. Important too, is an evaluation of the statistical records. To the extent that deficiences in this respect can be excluded, the factors regulating the populations can be attacked.

The comparison made between the two rivers Lule älv and Indalsälven indicate the importance of local factors. It does not confirm the hypothesis that the yearly fluctuations in these two rivers, as reflected in recorded salmon catch, are generally ruled by common factors. This statement needs re-examination by extending the investigation to more rivers and groups of rivers and comparison with other areas.

It is my hope to be able later to return to this subject with more positive results of field investigations and existing material, hydrological and biological, connected with the main problem, salmon stock fluctuations.

Acknowledgements

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Summary

In a recent paper in this series SVÄRDSON (1955) discusses the Baltic salmon fluctuations. Based upon correlation analyses between maximum ice cover in the Baltic sea area and a "salmon curve" or catch statistics from the Svartö weir in the river Lule älv the paper deals with 1. a mathematically demonstrated connection between mild ice conditions and increased river catch in the 3rd summer thereafter, 2. a mathematically demonstrated connection between severe ice conditions and increased river catch in the 6th summer thereafter, and 3. the large-scale catch fluctuations.

The catch in the Svartö weir has been assumed representative for the northern Baltic. This is not the case however.

In the mathematical treatment of the material due regard to its nature of "mixed connections of covariances" has not been payed. Those connections which are presumed to apply to secondary or yearly fluctuations are, therefore, no evidence of biological interrelations and the hydrological and biological arguments set forth for their interpretation are in essential details unverified and unlikely.

The causes of the dominating primary or large-scale fluctuation, including the porpoise hypothesis, are not sufficiently analyzed and the importance of the porpoise hunting in the Danish sounds appears to have been overestimated.

Addendum

Dr SVÄRDSON has kindly given me an opportunity to read his reply to this paper (published in this volume p. 357—384). Based upon the manuscript available to me, I want to state the following:

1. Only now does SVÄRDSON mention any deficiencies as regards the statistical material. He maintains, however, a biological foundation for the mathematical results but has now, without openly admitting it, abandonned his main explanations from 1955 to cases 2 and 3 (see footnote p. 117), the chief objects for my critizism, and replaced them by new ones, *viz.*

2. the causal chain: severe ice conditions in the Baltic — cold river water in spring — postponed smolt transformation — rich smolt class in the following year — good run from this class the 5th year after the severe winter, is replaced by the chain: severe ice conditions — cold coastal water in spring — slow growth of smolt after migration — prolonged time of exposure to predators — increased mortality in the coastal area — weak spawning run from this smolt year class — return to normal level ("apparent peak" acc. to SVÄRDSON) after 4—6 years. The whole discussion of smolt transformation is abandonned (which is unjustified; river temperatures etc. are at work even when not correlated with Baltic ice conditions, cf. p. 124). SVÄRDSON suggests a new definition of the concept of smolt class, including the coastal mortality after the termination of river life which would still enable him to speak about "smolt classes", but which is unacceptable,

3. the causal chain: mild ice conditions — increased growth in the sea — increased run after two years, is replaced by: mild ice conditions — warm coastal water — increased smolt growth on the coast — shortened time of exposure to predators — decreased mortality in the coastal area — increased run after 2—3 years. The original explanation serves, however, as a supplementary agent.

4. Both the new explanations rest upon one and the same hypothesis expressed in the first five links of the new chains. In principle, it may be or may not be correct but, nevertheless, in this case, it is only a hypothesis, though founded upon some general laws. (The smolt sojourn in the coastal area is probably very short. The mean difference between June sea-water temperatures after mild and severe winters are, in the Bothnian Sea, in the order of 1 C°. The coastal water temperature is, in a complicated way, influenced by river temperatures who, at time of smolt migration, are uncorrelated with Baltic ice conditions. There is no very firm basis, thus, for such farreaching consequences implying a masking or postponing of the large long-term fluctuation; a new suggestion by SVÄRDSON.)

5. The hypothesis is put forward as a new biological explanation of the mathematical findings on the Svartö data. (SVÄRDSON 1955 p. 235; here Table 5). The hypothesis must imply, *inter alia*, that average catches follow 2—3 years after average winters. The Svartö data demonstrate, however, bad catches 2—3 years after such winters. (A corresponding division into mild, average and severe winters is lacking in the new material presented by SVÄRDSON.) Thus, the hypothesis seems to fail as an explanation.

6. For the study of short-term fluctuations, I have proposed the elimination of the long-scale trend by the use of catch deviation figures (LINDROTH, 1950). A similar procedure is adopted by MILNE (1955, J. Fish. Res. Bd Can. 12: 451—485). Using it, with reference to the Svartö material (1835—1951), the following table is obtained.

Ice year relative to catch year	Baltic ice conditions mild	medium	severe
0	110	92	92
—1	91	104	105
—2	109	103	83
—3	108	87	99
—4	88	100	113
—5	94	107	99

This table, showing the mean corrected catch (as p.c. deviation from the 5-year catch means) 0—5 years after the winter categories used, is a sounder basis for discussing short-term fluctuations. In this connection, however, I confine myself to the statement that the trend in catch distribution on mild, medium and severe Baltic ice conditions for a certain year after the winters, in no instance coincides with the trends in SVÄRDSON's original table on uncorrected catch data. This stresses my critizism of SVÄRDSON's approach.

7. The important question of the conformity of the annual catch fluctuations between the different rivers (see p. 126) is not taken up.

8. Although frequently accused by SVÄRDSON (in his Swedish manuscript) of misunderstandings and errors, and although SVÄRDSON's recent paper is very open to critizism, I do not intend to burden the international discussion with a detailed reply. The observant reader will, I am sure, be able to judge for himself. Should anyone be especially interested, a Swedish memorandum (type-written) is available for loan from the author or at the Institute of Freshwater Research, Drottningholm, and the Migratory Fish Committee, Vattenfallsstyrelsen, Stockholm.

References

ALM, G. 1924. Laxen och laxfiskets växlingar i Mörrumsån och andra östersjöälvar. *Meddel. Lantbruksstyr. Stockholm 252: 1—134.*

— 1934. Salmon in the Baltic precincts. *Cons. intern. explor. mèr, Rapp. 92: 1—63.*

BEHRENDT, CHR. 1929. Om Marsvinsjæger-Lauget i Middelfart. *Turistforeningen for Danmark, Aarbog 1929: 235—252.*

BELDING, D. L. and J. A. KITSON, 1934. Spring-run and fall-run atlantic salmon. *Trans. Amer. Fish. Soc. 64: 225—230.*

BERG, S. 1957. Laxperioderna i Norrlandsälvarna. *Sv. Fiskeritidskrift 66: 6—7.*

BONNIER, G. and O. TEDIN, 1940. Biologisk variationsanalys. Stockholm.

EKMAN, S. 1938. Brehm: Djurens liv I. Stockholm.

HAGMAN, N. 1938. The variations in the catch of salmon and the water levels of the rivers. *Soc. Zool. Bot. Vanamo, Ann. Zool. 5: 1—45.*

IRMINGER, C. 1846. Marsvinsjagten i Lille Bælt, og Grindefangsten ved Færöerne. *Nyt. Arch. Sövæsenet, Köbenhavn. 2 (1): 27—42.*

JURVA, R. 1952. On the variations and changes of freezing in the Baltic during the last 120 years. *Soc. Geogr. Fenn. 75: 17—24.*

JACOBSEN, J. P. and A. C. JOHANSEN, 1921. On the causes of the fluctuations in yield of some of our fisheries. I. The salmon and sea trout fisheries. *Meddel. Komm. Havundersög., Fiskeri 6 (5): 1—48.*

JOHANSEN, A. C. 1929. Om dödligheden blandt Marsvin, Fisk og större Krebsdyr i Farvandene omkring Danmark under strenge Vintre. *Dansk Biol. Stat., Beretn. 35: 59—91.*

LILJEQUIST, G. 1943. The severity of the winters at Stockholm 1757—1942. *Stat. Meteor. Hydrol. Anst., Meddel. 46: 1—24.*

LINDROTH, A. 1950. Laxbeståndets fluktuationer i de norrländska älvarna. *Sv. Vattenkraftfören. Publ. 415: 99—224.*

— 1955. Mergansers as salmon and trout predators in the river Indalsälven. *Rept. Inst. Freshw. Res. Drottningholm, 36: 126—132.*

— 1957. Laxodlingsprogrammet för det närmaste decenniet. *Sv. Vattenkraftfören. Publ. 460: 199—216.*

MACINTYRE, D. 1934. Sea enemies of salmon. *Salmon and Trout Mag. 74: 38—42.*

MØHL-HANSEN, U. 1954. Investigations on reproduction and growth of the porpoise (*Phocaena phocaena* (L.) from the Baltic. *Dansk naturhist. Foren., Vidensk. Meddel. 116: 369—396.*

NORDQVIST, O. 1906. Laxens uppstigande i Finlands och norra Sveriges elfvar. *Fennia 22: 1—58.*

— 1924. Times of entering of the atlantic salmon in the rivers. *Cons. intern. explor. mèr, Rapp. 33: 1—58.*

OLOFSSON, O. 1935. Laxfisket i övre Norrland år 1934. *Sv. Fiskeritidskrift 44: 31—35.*

PALOSUO, E. 1953. A treatise on severe ice conditions in the central Baltic. *Havsforskningsinst. Skr. 156: 1—130.*

SCHEURING, L. 1929—1930. Die Wanderung der Fische. *Ergebn. Biol. 5: 405—691; 6: 4—304.*

SHAPOVALOV, L. and A. TAFT, 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*). *Calif. Fish Bull. 98: 1—375.*

SVÄRDSON, G. 1955. Salmon stock fluctuations in the Baltic Sea. *Rept. Inst. Freshw. Res. Drottningholm, 36: 226—262.*

TAUBER, P. 1892. Pattedyr. Zoologia Danica 1 (8). Kbhvn.

TRYBOM, F. 1908. Ichthyologische Beobachtungen auf den Laichplätzen der Lachse und Meerforellen im Unterlauf des Flusses Dalelf in Schweden. *Sv. Hydr. Biol. Komm. Skr. 3: 1—13.*

ÖSTMAN, C. J. 1937. Isförhållandena vid Sveriges kuster. *Stat. Meteor. Hydrol. Anst., Meddel. 6 (6): 1—63.*

Sur les planctons crustacés de la zone littorale

Par THOROLF LINDSTRÖM

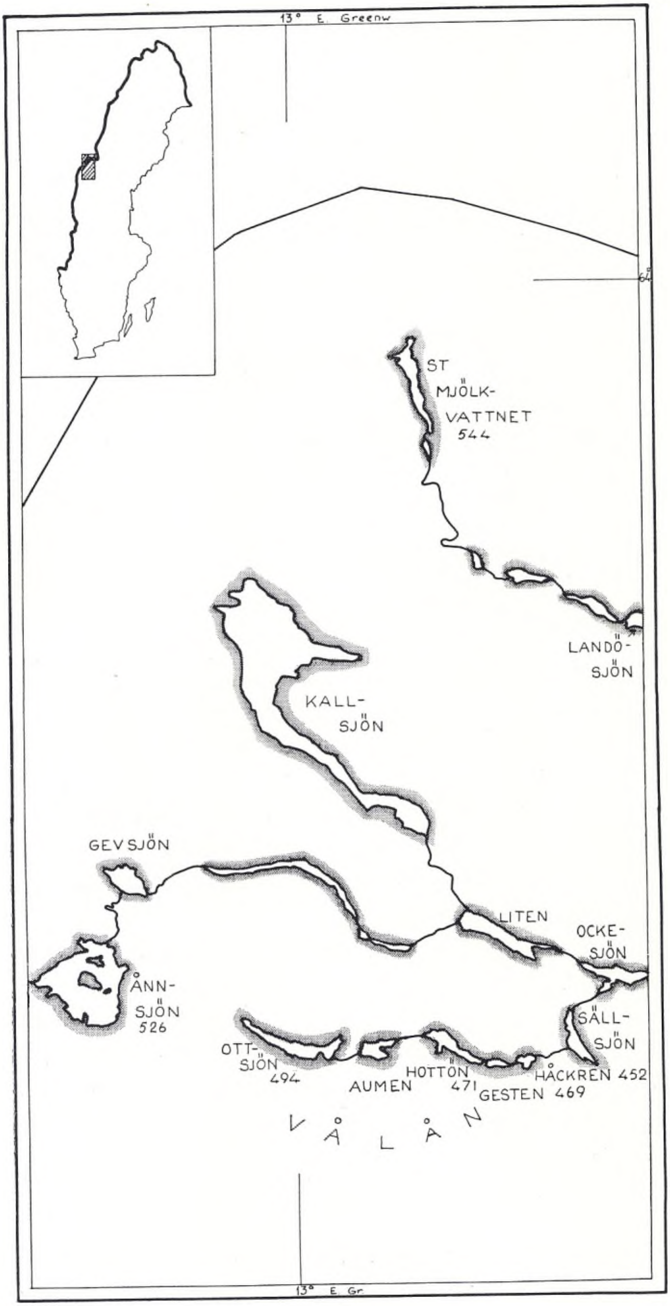
Addendum: Remarks concerning the flow through Lake Håckren par G. NYBRANT

Introduction

Aux environs de 1900 la discussion portrait sur les particularités inhérentes aux planctons de la région littorale (vadale) et à ceux de la région pélagique (limnétique); de même que sur les échanges qui s'effectuaient entre ces deux régions; et l'on se demandait s'il était légitime de fixer les limites entre ces régions. (ZACHARIAS 1893, FRANCÉ 1894, APSTEIN 1896, BIRGE 1897, STENROOS 1898, ZSCHOKKE 1900, STEUER 1901).

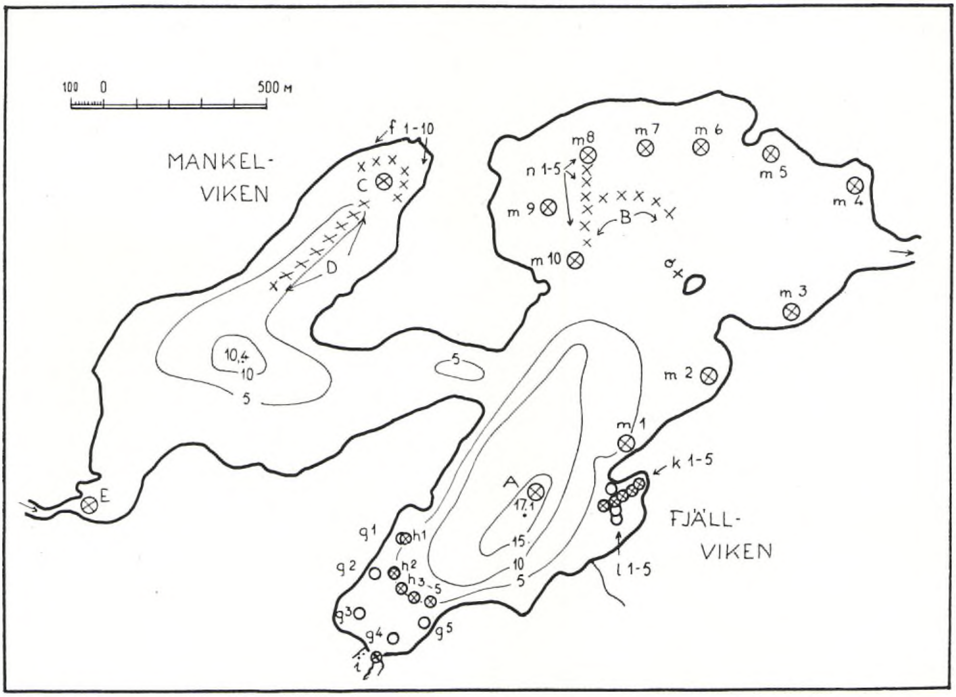
La région littorale s'est souvent montrée pauvre en planctons crustacés (KOROTNEFF 1904, BURCKHARDT 1910, SOUTHERN et GARDINER 1926, RUTTNER 1930, LINDSTRÖM 1952). Les *Polyphemus* et les *Bosmina* sont spécialement classés comme plancton de littoral et on souligne qu'ils se trouvent aussi dans les étangs et que comme tous les planctons crustacés du littoral ils se rencontrent souvent en essaims. (STENROOS 1895, APSTEIN 1896, LILLJEBORG 1900, EKMAN 1904, HUITFELT KAAS 1906, SCHNEIDER 1908, LANGHANS 1911, NORDQUIST 1921, SOUTHERN et GARDINER 1926, STRØM 1926, TER PORGHOSSIAN 1928, AURICH 1933, LIEDER 1950, THOMASSON 1952, LINDSTRÖM 1952, FINDENEGG 1953).

Les eaux courantes sont pauvres en planctons crustacés. Les régions des grands fleuves où l'on trouve une richesse de planctons crustacés sont surtout situées dans les branches secondaires là où le courant se ralentit ou encore, dans les poches qui se rencontrent le long du cours des fleuves. D'autre part, pour les lacs, plus leur débit est grand, comparé à la grandeur de leur bassin, plus ils sont pauvres en planctons. (SCHRÖDER 1898, ZACHARIAS 1898, KOFOID 1903, 1908, HUITFELT KAAS 1906, STEUER 1910 avec bibliographie, BREHM 1911, SOUTHERN et GARDINER 1926, AURICH 1933, A. BURCKHARDT 1935, REIF 1939, PENNAK 1946, avec bibliographie, BALDI 1950, LINDSTRÖM 1952, BROOK et WOODWARD 1956).



Carte 1. Carte générale. Les chiffres indiquent l'altitude.

Se basant sur de telles observations, **Burckhardt**, en 1910, établit l'hypothèse suivante: Plus les planctons ont de chemin à parcourir pour leur migration diurne, moins on a de chance d'en trouver dans les régions littorales. Il soulignait aussi que leur rareté était plus grande encore dans la zone lit-



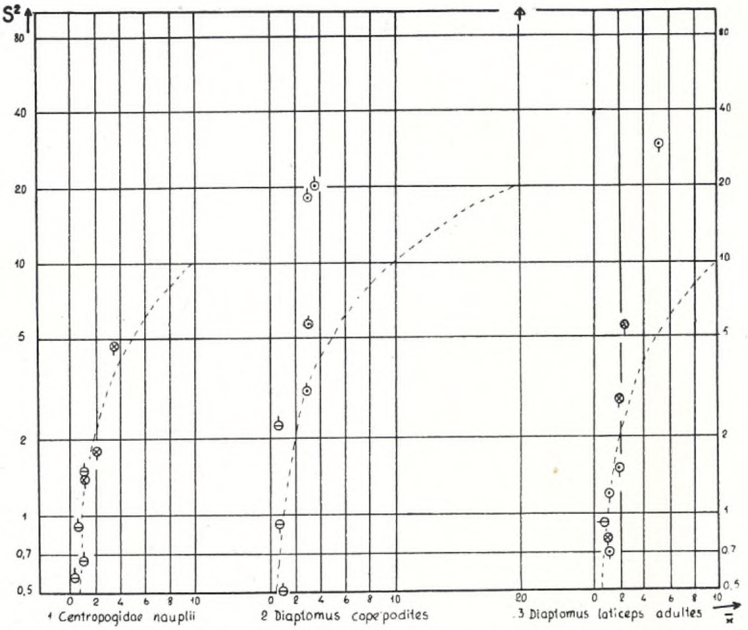
Carte 2. Håckren. Carte bathymétrique, selon NYBRANT, dans la même publication. Les lettres ajoutées désignent les stations où les épreuves de planctons ont été prises.

torale si le profil du fond du lac présentait de brusques dénivellations ou si la zone littorale était très étendue. Ce mécanisme qui est cause de la pauvreté en planctons dans les eaux peu profondes, produit le même effet disait-il sur la densité des planctons dans les émissaires des lacs.

Dans une étude précédante nous avons préliminairement discuté, en 1952, de l'abondance des planctons crustacés dans la zone littorale. Afin de poursuivre l'étude de l'abondance des planctons dans les petits lacs et dans la zone littorale, nous avons choisi le lac Håckren. L'analyse planctonique de la partie profonde du lac n'est pas encore terminée, mais nous ne traiterons aujourd'hui que des régions peu profondes. Pour systématique, méthode et instruments de travail voir op. cit. 1952.

Relation entre la moyenne et la variance

Pour établir la variance qui caractérise chaque série d'observations sur l'abondance des planctons crustacés, nous nous sommes servis du matériel non-publié, du matériel publié en 1952, et de celui qui entre dans les tableaux joints à cette étude. Les épreuves, pour chaque valeur de variance dans les graphiques sont prises au même temps, à la même station et à la même pro-



Graphique 1.—8. Variance intraclasse et moyennes. Le volume d'épreuves est de 5 l., sauf dans Hottön en 1954 (5,3 l.).

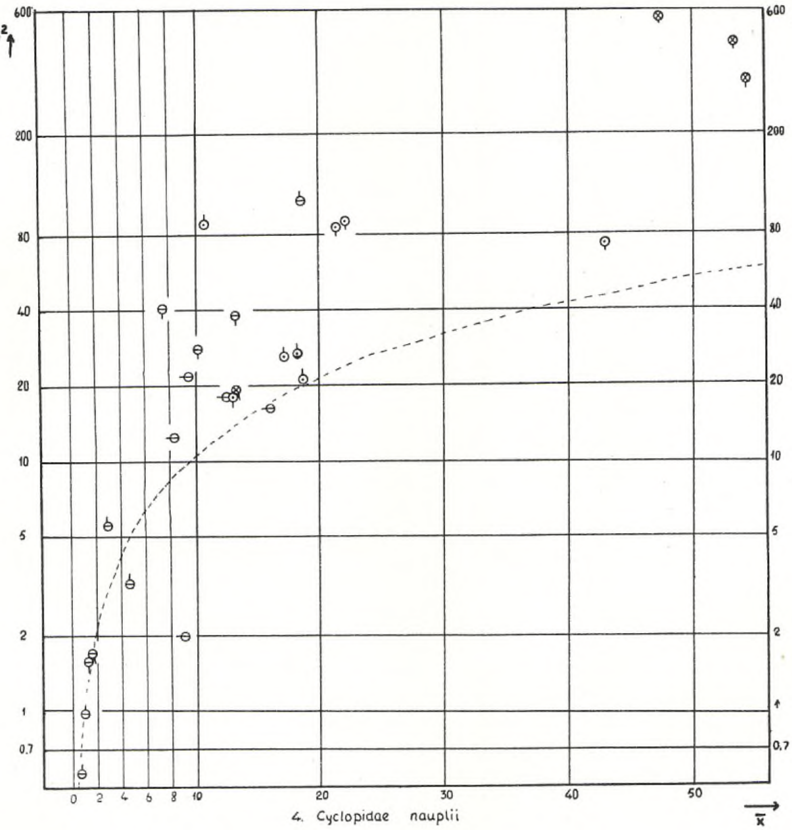
Légende:

	♁ **Mai**	♀ **Août**	⊸ **Octobre**
⊖ **Hottön 1948**	⊖ **nomb. épreuv.=7**	⊖ **n= 4**	⊖ **n=4**
△ **Hottön 1954**		△ **n=21**	
⊙ **Ottsjön 1948**	⊙ **n=10**	⊙ **n= 5**	
⊗ **Ånn 1948**		⊗ **n= 6**	

Ce qui suit n'est pas noté dans les graphiques:

⊖ **graph. 4** $\bar{x}=$ **12,8** $S^2=$ **0,25**
△ » **7** »**=133,5** »= **2613**
△ » **8** »**=445** »**=291210**

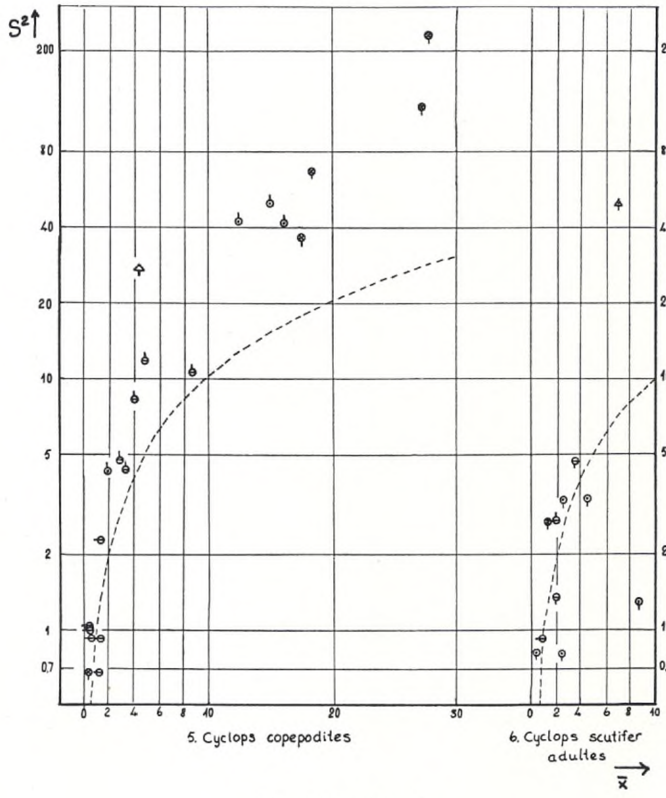
fondeur. Chaque forme de planctons a été traitée à part. Il ressort du graph. 1—8 que la valeur de la variance se rapproche de la valeur de la moyenne aussi longtemps que celle-ci est basse, mais elle remonte beaucoup plus rapidement que celle de la moyenne (BARNES et BAGENAL 1951, BARNES et MARSHALL 1951). Dans une distribution de Poisson, la variance égale la moyenne (courbe faite d'une suite de traits dans les graphiques. Le matériel de 1948 pris dans Hottön, Ottsjön et Ånn ainsi que le matériel de Hottön pris à minuit entre le 2 et 3 août 1954, ont été analysés par *Le Service de la statistique de l'Université de Stockholm.* Lorsque furent prises les épreuves de minuit, le



Graphique 4.

temps était à peu près calme mais l'abondance des planctons était due sans doute à l'influence des migrations diurnes qui s'effectuaient lorsque furent prises les épreuves. Il est difficile d'éliminer la source d'erreurs des grandes séries d'épreuves. Le service de la statistique a conclu que dans quelques cas seulement, lorsque la moyenne est assez basse, on peut accepter l'hypothèse d'une distribution de Poisson; dans les autres cas la variance est trop grande.

Dans les graphiques 1—8 chaque valeur, porte un signe distinctif pour chaque époque différente. Les résultats obtenus par ce traitement préliminaire du matériel n'encourageaient pas une analyse plus approfondie. RICKER 1938 et LANGFORD 1938 ont rendu-compte des types de distributions qui caractérisent les différentes espèces de zooplanctons. La confrontation de leurs résultats et des nôtres nous laisse à penser qu'il est difficile de donner une caractéristique valable en toutes circonstances au moyen de la variance. Si dans une distribution les animaux sont plus ou moins aggregés ou plus ou moins espacés, cela est du aux mouvements propres aux animaux (Cf. BAINBRIDGE 1953) et au mouvements de l'eau. Le type de distribution peut varier



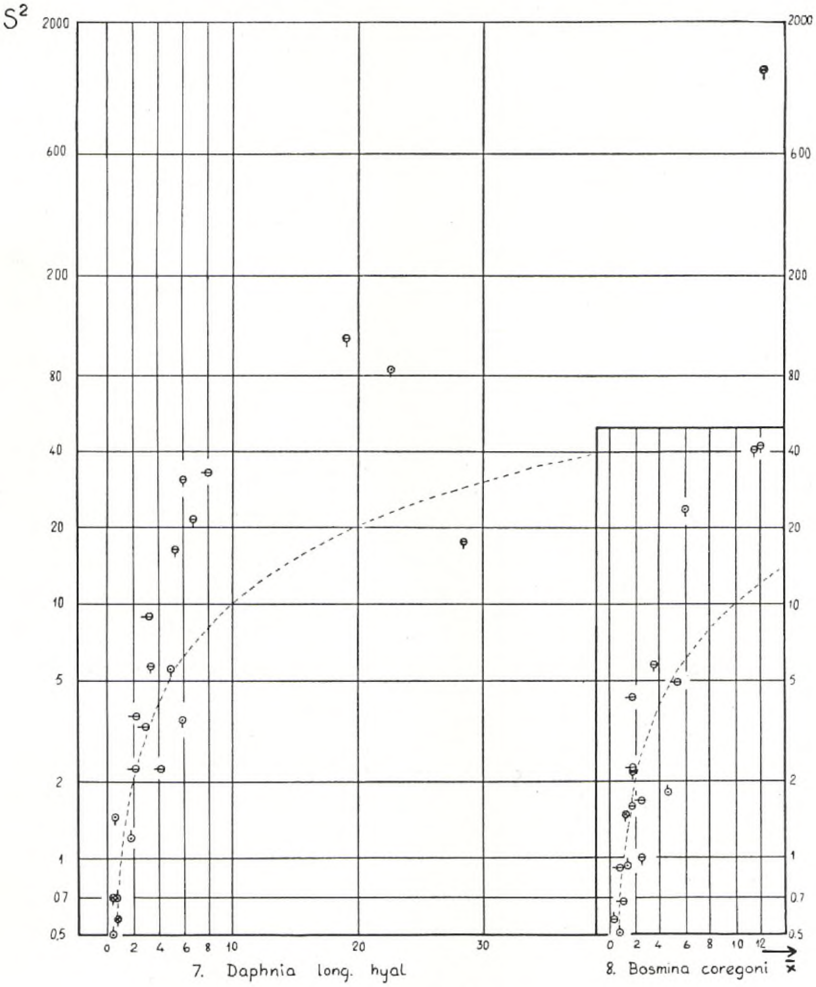
Graphique 5—6.

radicalement en un court espace de temps. L'écart, entre des variances élevées et basses, pour une certaine espèce et une certaine moyenne, est grand, lorsque la moyenne est élevée.

Les valeurs des variances de la zone littorale (graphique 9) sont toutes élevées. On ne peut prouver, avec ce materiel, l'hypothèse que la variance intraclasse est la plus haute dans la région littorale et dans des petits bassins bien abrités; car il n'y a que des séries peu nombreuses dans la région pélagiale des grands lacs où la moyenne est grande.

Abondance des planctons dans des régions peu profondes (3 mètres au maximum)

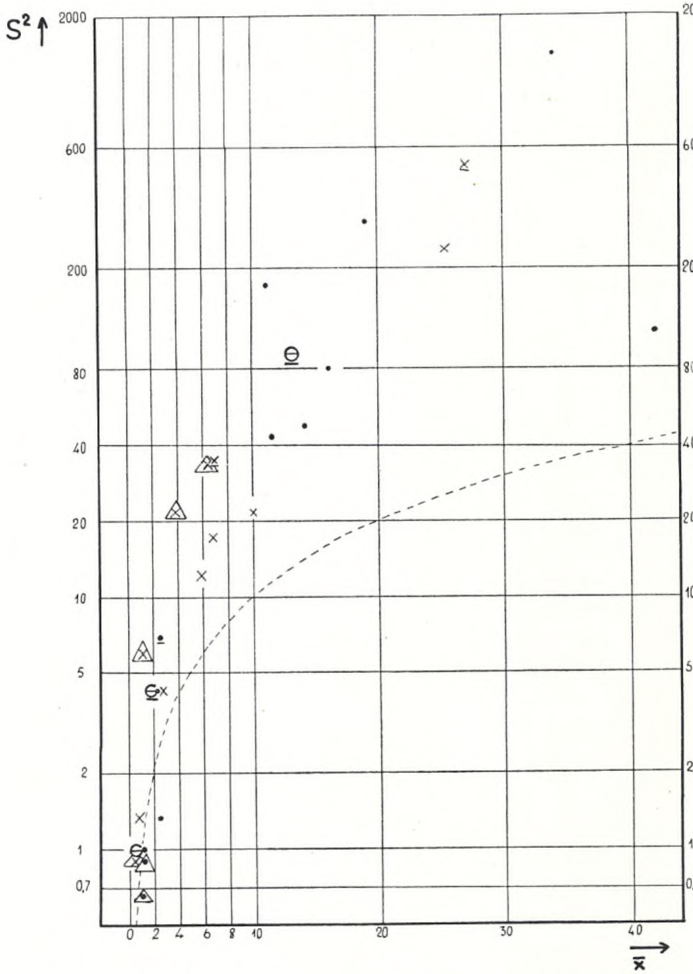
Pour illustrer le cycle annuel des régions peu profondes, c'est à dire ne dépassant pas trois mètres de profondeur, nous avons établi le tableau 1 et le tableau 2, ce dernier tableau ne contient que des épreuves prises au mois d'août mais il comporte aussi des épreuves prises à d'autres profondeurs. Si l'on compare ce matériel à celui du bassin plus profond, en partie publié



Graphique 7—8.

en 1952, en partie non-publié, on constate une pauvreté de *Diaptomus*, de *Cyclops scutifer*, et de *Daphnia* durant le mois d'août, dans les régions peu profondes. Celles-ci sont aussi personnifiées par la présence de *Bosmina* et de *Polyphemus*; la densité en *Bosmina* est quelquefois assez élevée, mais cette espèce étant nombreuse aussi dans les épreuves prises dans le bassin plus profond, le 17. 8. 1951, on ne peut pas dire que dans les régions littorales la densité est la plus haute. Tout ceci corrobore les résultats obtenus auparavant. Une juxtaposition des résultats publiés en 1952 est faite dans le graphique 10. La mesure de la probabilité pour les comparaisons n'a pas été faite; la valeur de preuve que pourrait présenter le matériel se trouve dans le fait que les mêmes caractéristiques reviennent d'un lac à l'autre.

Dans op. cit. 1952, nous avons montré que les épreuves prises près de la



Graphique 9. Variance intraclasse et moyenne, pour les Cladocères, en août. Le matériel du bassin central de Håckren, en parti publié en 1952, en parti non-publié, volume=5,3 l., nombre d'épreuves=3. Le matériel de la région littorale des lacs Gesten, Hottön et Ottsjön, publié en 1952 (c.f. graph. 10) volume: 5,3 l. ou 5 l., nombre d'épreuves=entre 3 et 5.

Légende:

	bassin de Håckren	Région littorale Epreuves de 5 l.	Région littorale Epreuves de 5,3 l.
Daphnia long. hyal.	●	●̲	◬
Bosmina corégoni	×	×̲	⨻
Polyphemus pédiculus..		⊖̲	⊖

Ce qui suit n'est pas noté dans le graphique:

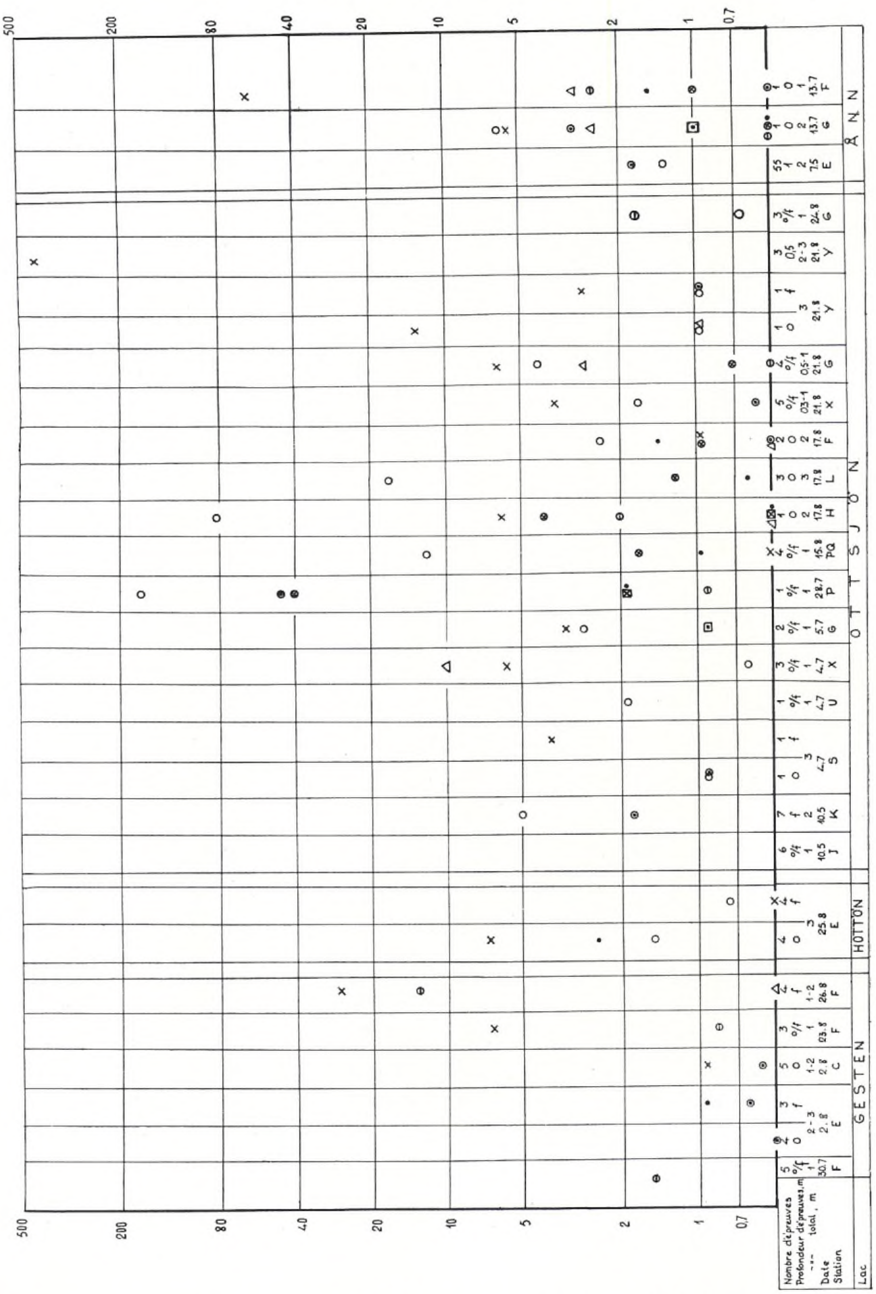
	$\bar{x}$	S^2
●	153	2810
●	147	7413
●	66	542
●	50	6231
×	150	43216
×	11	0,33
⨻	460	535000

Tableau 1. Le cycle annuel dans Håckren. Légende pour les tableaux 1, 2, 4 et 5:

$\bar{x}$=moyennes pour les épreuves d'un volume de 5,3 litres.
$\bar{x}_5$=la moyenne recalculée pour cinq litres.
s^2=variance.
0=épreuves de surface.
f=épreuves prises près du fond.
o/f=la profondeur d'épreuves non-spécifiée.

Date	2.6.55			8.6.55			22.6.55			3.7.55		
Heure	16 h—19 h			17 h—18 h 30			13 h 30—14 h 30			15 h—16 h		
Station	m 1—10			m 7—8			m 6—10			m 6—10		
Profondeur totale, en métres	1,5—2			2			2			2		
» des épreuves	f			f			f			f		
Nombre des épreuves	10			10			5			5		
	$\bar{x}$	s^2	$\bar{x}_5$	$\bar{x}$	s^2	$\bar{x}_5$	$\bar{x}$	s^2	$\bar{x}_5$	$\bar{x}$	s^2	$\bar{x}_5$
Centropagidae nauplii	1,8	3,1	1,7	3,1	2,5	2,9	1,0	1,5	0,95	1,0	1,5	0,95
Diaptomus copépodites	—	—	—	—	—	—	—	–	—	1,0	0,50	0,95
Cyclopidae nauplii	3,5	21	3,3	3,6	4,0	3,4	0,80	1,7	0,76	1,2	2,7	1,1
Cyclops copépodites I—III	3,9	24	3,7	6,8	16	6,4	1,6	1,3	1,5	1,4	1,8	1,3
» » IV—V	0,20	0,18	0,19	0,30	0,23	0,28	0,40	0,30	0,38	1,2	1,7	1,1
Cyclops scutifer adultes	—	—	—	—	—	—	—	—	—	0,20	0,20	0,19
Daphnia long. hyal. ♀♀ jeunes	—			0,10			—			0,20		
» » » ♀♀ adultes	—	—	—	—	0,10	0,09	—	—	—	—	0,20	0,19
» ♂♂	—			—			—			—		
Bosmina coregoni	0,40	0,71	0,38	0,80	1,1	0,76	0,40	0,30	0,38	1,2	1,7	1,1

surface à l'endroit de la plus grande profondeur, étaient pauvres en *Cyclops,* en *Daphnia* et en *Bosmina* (cf. FUHRMAN 1900), sauf les jours de grand vent. Nous avons essayé de faire une estimation du vent en 1955, dans Håckren, mais la force du vent n'a jamais été suffisante pour être bien évaluée avec l'appareil dont nous disposions, elle n'a jamais dépassé un ou deux mètres à la seconde. Les épreuves prises à la station n 1—5, le 10. 8. 1955 (tableau 2, 3) indiquent que l'eau de surface est pauvre, même dans les régions littorales. Il en est de même pour les *Bosmina* dans le Gesten, station E, et dans Ottsjön, station S, dont nous avons rendu-compte dans le graphique 10. Cette indication n'est pas entièrement concluante, elle est contredite par les épreuves prises dans Hottön E et Ottsjön Y, portées dans le même graphique. Nous n'avons pas précisé ordinairement la profondeur où nous avons pris les épreuves lorsque la profondeur totale ne dépasse pas un mètre; nous avons seulement placé le signe: o/f. Cependant à la station f, du lac Håckren, (13. 8. 1955) tableau 2, nous avons pris cinq épreuves aussi près que possible de la surface et cinq autres aussi près que possible du fond. Le résultat porte à penser qu'il faut accepter le fait d'une eau de surface plus pauvre en *Bosmina* que celle du fond, même pour les stations où la profondeur ne dépasse pas un mètre, seulement la variance est si grande que la forte différence entre les moyennes n'est pas significative du point de vue conventionnel (tabl. 3). Si les chiffres initiaux sont logarithmées, p. devient 0,2—0,05*.



Graphique 10. Les moyennes sont calculées pour un volume de 5 l. pour les planctons crustacés des épreuves littorales dont il a été rendu-compte en 1952. Les moyennes en dessous de 0,5 sont omises. o=épreuves de surface, f=épreuves prises près du fond, o/f=profondeur non-précisée. Les stations peuvent être retrouvées sur les cartes publiées en 1952.

Légende:

Cyclop. nauplii ○
Cyclops copépodites ⊙
» scutifer adultes ⊗

Centrop. nauplii □
Diaptomus copépodites ⊡
» laticeps adultes ☒

Daphnia long. hyal. •
Bosmina coregoni ×
Polyphemus pediculus ⊖
Autres crustacés △

Tableau 2. Répartition verticale du plancton littoral dans Håckren. Différence entre les stations d'une profondeur totale au dessus et en dessous de 3 mètres. Pour les abréviations voir tableau 1.

Date	10.8.55						11.8.55					
Heure	13 h—14 h						11 h 30			12 h 30		
Station	n 1—5						g 1—5			h 1—5		
Profondeur totale, en métres	1,5—2,5						0,75—1,5			4—6		
» des épreuves, m	0			f			0/f			2		
Nombre des épreuves	5			5			5			5		
	$\bar{x}$	s^2	$\bar{x}_5$	$\bar{x}$	s^2	$\bar{x}_5$	$\bar{x}$	s^2	$\bar{x}_5$	$\bar{x}$	s^2	$\bar{x}_5$
Diaptomus copépodites	—	—	—	—	—	—	—	—	—	—	—	—
Cyclopidae nauplii	0,40	0,30	0,38	1,6	13	1,5	0,40	0,80	0,38	—	—	—
Cyclops copépodites I—III	—	—	—	2,4[1]	23	2,3	—	—	—	0,20	0,20	0,19
» » IV—V	—	—	—	1,4[1]	9,8	1,3	—	—	—	—	—	—
Cyclops scutifer adultes	0,20	0,20	0,19	1,2[1]	4,7	1,1	—	—	—	0,20	0,20	0,19
Daphnia long. hyal. ♀♀ jeunes	0,80			—			—			—		
» » » ♀♀ adultes	—	1,7	0,75	0,20	0,20	0,19	—	—	—	49	4.903	47
» ♂♂	—			—			—			1,0		
Bosmina coregoni	2,0	2,0	1,9	4,0	6,5	3,8	16	1.187	15	23	1.912	22
Polyphemus pediculus	0,20	0,20	0,19	—	—	—	2,8	35	2,6	0,40	0,30	0,38
Autres crustacés	0,20	0,20	0,19	2,0	9,6	1,9	0,40	0,80	0,38	—	—	—

Date	13.8.55						13.8.55								
Heure	12 h—14 h						12 h—14 h								
Station	f						D								
Profondeur totale, en métres	1						5,5—6								
» des épreuves, m	0			f			1			2			f		
Nombre des épreuves	5			5			3			3			3		
	$\bar{x}$	s^2	$\bar{x}_5$	$\bar{x}$	s^2	$\bar{x}_5$	$\bar{x}$	s^2	$\bar{x}_5$	$\bar{x}$	s^2	$\bar{x}_5$	$\bar{x}$	s^2	$\bar{x}_5$
Diaptomus copépodites	—	—	—	—	—	—	0,33	0,33	0,31	—	—	—	—	—	—
Cyclopidae nauplii	0,20	0,20	0,19	—	—	—	0,67	0,33	0,63	—	—	—	3,0	27	2,8
Cyclops copépodites I—III	—	—	—	—	—	—	—	—	—	1,0	0,50	0,95	3,7	10	3,5
» » IV—V	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cyclops scutifer adultes	—	—	—	—	—	—	—	—	—	—	—	—	0,33	0,33	0,31
Daphnia long. hyal. ♀♀ jeunes	—			0,20			24			23			92		
» » » ♀♀ adultes	0,60	0,70	0,57	0,80	1,5	0,95	134	8.784	152	245	25.880	253	75	26.791	159
» ♂♂	—			—			2,3			27			1,0		
Bosmina coregoni	21	711	0,20	110	21.142	104	1,3	1,3	1,2	1,0	1,0	0,95	8,7	225	8,2
Polyphemus pediculus	4,6	10	4,3	1,0	5,0	0,95	—	—	—	0,67	1,3	0,63	—	—	—
Autres crustacés	—	—	—	—	—	—	0,33	0,33	0,31	0,67	0,33	0,63	—	—	—

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[1] La pluspart ne sont pas scutifer.

Tableau 3. La repartition verticale des Bosmines dans la région littorale.

Date	Station	$\bar{x}_{surface}$	$\bar{x}_{fond}$	variance »entre les profondeures« / variance intraclasse	P
10.8.55	n 1—5	2,0	4,0	2,35	0,1—0,2
13.8.55	f	21	110	1,80	0,2—0,3

Abondance des *Daphnia* là où la profondeur totale a moins ou plus de 3 mètres

Les résultats publiés auparavant au sujet de la distribution des differentes formes de *Daphnia* aux différentes profondeurs, au mois d'août, se trouvent confirmés par les nouvelles observations faites dans le grand bassin de Håckren, et dans le bassin moins profond de Mankelviken (cf. tableau 2, station D, le 13. 8. 1955, cf. aussi EDMONDSSON 1955). Le rassemblement des *Daphnia* adultes à deux mètres de profondeur se retrouve aussi dans des stations moins profondes (station D, 1—2 mètres en dessous de la surface) mais la profondeur totale doit dépasser trois mètres. Ceci est illustré par une épreuve de la station k 1—5 du 10. 8. 1955, tableau 4 et aussi par les épreuves de la station g 1—5 et h 1—5 du 11. 8. 1955, tableau 2. Dans ce dernier cas il n'est pas possible de calculer un quotient de la variance, car il n'y avait pas d'adultes dans les épreuves des stations moins profondes. Si délaissant le fait de la grande supériorité de la moyenne dans la région la plus profonde, on se contente pour le calcul du nombre d'épreuves avec ou sans *Daphnia* des deux séries, le χ^2 pour l'hétérogénéité devient 6, 7**. Si on calcule la probalité de l'hypothèse d'une même population pour les deux séries, selon la méthode décrite par FISCHER 1950, page 96—97, la valeur p devient 0,024, c'est à dire que la différence entre les séries n'est pas aussi significative. Si l'on tient compte des observations précédantes au sujet des rassemblements de *Daphnia* adultes à deux mètres de profondeur, et de leur pauvreté en surface dans les régions pélagiques des lacs, la différence entre les deux séries doit être considérée comme réellement significative.

Migrations nocturnes obliques vers les régions peu profondes

Puisqu'il y a abondance de *Daphnia* dans les bassins du lac, qu'il y a peu de *Daphnia* pendant le jour, dans les régions dont la profondeur ne dépasse pas trois mètres, on pourrait envisager l'existence d'une migration nocturne vers les eaux moins profondes alors que les *Daphnia* remontent, et, une émigration dans les premières heures de la matinée, et que ces mouvements pourraient exister aussi pour d'autres espèces. Pour élucider cette question nous avons pris les épreuves dans les stations l et k dont nous avons rendu-

Tableau 4. Migrations nocturnes obliques dans Håckren. Pour les abréviation voir tableau 1.

Date	9.8.55			15.8.55			10.8.55						9.8.55			10.8.55		
Heure	22 h			01 h 30			12 h 30—14 h 30						22 h 30			13 h—14 h		
Station	k 1—5			l 1—5			k 1—5						n 1—5			n 1—5		
Profondeur totale, en métres	0,5—4			2—3			0,5—4						1,5—2,5			1,5—2,5		
» des épreuves	0			0			0			f			0			0			f
Nombre des épreuves	5			5			5			5			5			5			5
	$\bar{x}$	s^2	$\bar{x}_5$	$\bar{x}$	s^2	$\bar{x}_5$	$\bar{x}$	s^2	$\bar{x}_5$	$\bar{x}$	s^2	$\bar{x}_5$	$\bar{x}$	s^2	$\bar{x}_5$	$\bar{x}$	s^2	$\bar{x}_5$	$\bar{x}$	s^2	$\bar{x}_5$
Cyclopidae nauplii	0,20	0,20	0,19	—	—	—	—	—	—	—	—	—	—	—	—	0,40	0,30	0,38	1,6	13	1,5
Cyclops copépodites I—III	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2,4[2]	23	2,3
» » IV—V	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1,4[2]	9,8	1,3
» adultes	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,20	0,20	0,19	1,2[2]	4,7	1,1
Daphnia long. hyal. ♀♀ jeunes	—			—			—			0,20			0,60			0,80			—		
» » » ♀♀ adultes	—	—	—	—	0,20	0,19	0,20	0,20	0,19	29[1]	4249	28	0,40	0,50	0,95	—	1,7	0,75	0,20	0,20	0,19
» ♂♂	—			0,20			—			—			—			—			—		
Bosmina coregoni	—	—	—	—	—	—	—	—	—	—	—	—	4,8	15	4,5	2,0	2,0	1,9	4,0	6,5	3,8
Polyphemus pediculus	0,20	0,20	0,19	—	—	—	0,40	0,80	0,38	0,20	0,20	0,19	0,20	0,20	0,19	0,20	0,20	0,19	—	—	—
Autres crustacés	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,20	0,20	0,19	2,0	9,6	1,9

[1] Tous les 146 Daphnies adultes provenant d'une épreuve de 2 *m.* au dessus d'une profondeur totale de 4 m. Profondeur totale pour les autres épreuves 0,5—2,5 m.

[2] La pluspart ne sont pas scutifer.

compte dans le tableau 4. Le résultat ne stimule pas à entreprendre des investigations plus poussées.

Planctons des eaux courantes et des courants d'eau

Rien n'indique qu'une migration diurne oblique vers les eaux peu profondes, dans le cas ou elle existerait, serait décelable à la station n 1—5 (tableau 4). Toute la baie qui s'étend vers le Nord-Est est une région très étendue et dont la profondeur connue n'atteint pas plus de trois mètres. Le plus proche bassin à grande profondeur de Håckren est celui de Fjällviken. Pour venir de Fjällviken à la baie Nord-Est, les animaux doivent passer à travers un courant d'eau qui joint le détroit à l'émissaire, selon une analyse faite par NYBRANT, qui se trouve dans la même publication, de sorte qu'une telle migration est peu probable.

Dans notre travail en 1952, les épreuves prises au centre de la baie Nord-Est (Station B), le 31. 7. et le 17. 8. 1951, étaient si pauvres que nous soupçonnons l'influence d'un courant d'eau qui pourrait exister à proximité ou à l'endroit même. Le développement du *Potamogeton* dans des courants d'eau à l'intérieur des lac est très riche dans plusieurs régions du système fluvial de Vålån. Il en est ainsi après l'arrivée de l'affluent et dans le détroit du lac Håckren, où de longues plantes s'inclinent dans la direction du courant. Dans les station o et B cette végétation n'existe pas avec un telle richesse, loin de là. Nous avons à faire à une section peu profonde et plus large que celle du détroit (Carte 2) et puisque le dèbit moyen par été normal est de 52 m^3/sec., on peut pourtant présumer que le courant d'eau est véritablement appréciable autour des stations o et B. C'est pourquoi nous avons pris la série d'épreuves de la station o et m 1—10, le 2. 6. 1955, (tableau 5 et 1). Si l'on calcule une moyenne par épreuve de toutes les formes, on obtient 0,90 et 9,8 et le quotient des variances se rapportant à la différence entre les deux moyennes des deux séries, devient 8, 7**. Des six formes de zooplanctons, cinq ont la moyenne la plus basse de la série de la station o. Cela concorde avec les faits souvent observés, à savoir que l'eau courante et les lacs à grands débits, sont pauvres en planctons crustacés.

Aux épreuves de Ottsjön, station R, le 15. 8. 1950 et Z, Å, Ä, le 21. 8. 1950, Gesten, station G, le 30. 7. 1951 et Håckren, station E, le 31. 7. 1951, dont il a été rendu-compte auparavant (op. cit. 1952), il faut ajouter celles que nous avons prises dans les affluents de Håckren, stations E et i ainsi que celles de l'émissaire de Mjölkvattnet pour élucider le mécanisme qui rend les eaux courantes pauvres en planctons (cf. BROOK et WOODWARD, 1956). On ne peut encore tirer que des conclusions préliminaires. Les *Bosmina,* les *Cyclops* nauplii, copépodites et adultes, sont le plus souvent emmenés, des lacs du système fluvial de Vålån dans les émissaires (Ottsjön, station Z, Å, Ä, Gesten, sta-

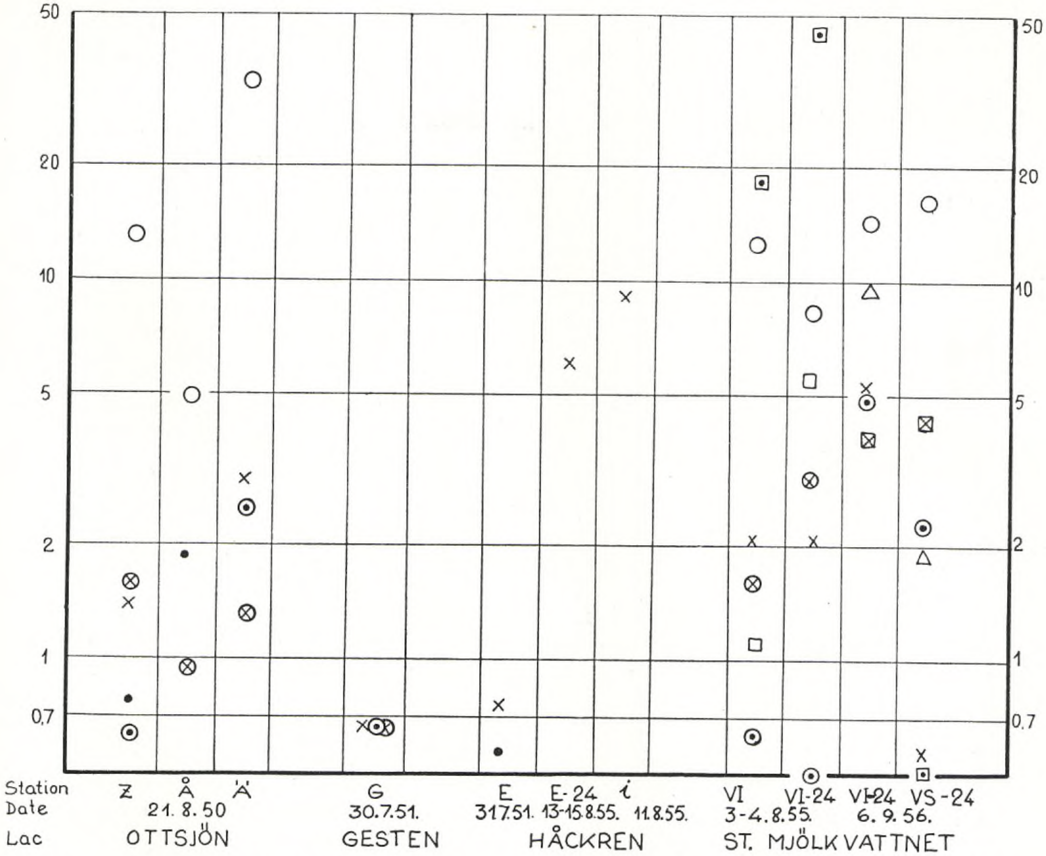
Tableau 5. Planctons dans les affluents et émissaires et courants d'eau. V.i. = Vanne inferieure, V.s. = Vanne supérieure. Autres abréviations: voir tabl. 1.

Lac	HÅCKREN							ST. MJÖLKVATTNET							
Date	2.6.55			13, 15.8.55		11.8.55		3—4.8.55				6.9.56			
Heure	18 h			15 h, 21 h, 02 h, 09 h,		11 h 30		12 h		20 h, 23 h 30 4 h 45, 8 h 30 12 h, 16 h		6 h, 12 h 30, 20 h 30			
Station	o			E		i		V. i		V. i		V. i.		V. S.	
Profondeur totale, en métres	2														
» des épreuves	f														
Nombre des épreuves	10			20		1		6		6		9		10	
	$\bar{x}$	s^2	$\bar{x}_5$	$\bar{x}$	$\bar{x}_5$	x	x_5	$\bar{x}$	$\bar{x}_5$	$\bar{x}$	$\bar{x}_5$	$\bar{x}$	$\bar{x}_5$	$\bar{x}$	$\bar{x}_5$
Centropagidae nauplii	0,30	0,23	0,28	—	—	—	—	1,2	1,1	6,0	5,7	—	—	—	—
Diaptomus copépodites	—	—	—	—	—	—	—	20	19	50	47	0,11	0,10	0,50	0,47
Diaptomus laticeps adultes	—	—	—	—	—	—	—	—	—	—	—	0,11	0,10	0,30	0,28
Diaptomus laciniatus adultes	—	—	—	—	—	—	—	—	—	—	—	4,0	3,8	4,4	4,1
Cyclopidae nauplii	0,30	0,46	0,28	0,05	0,05	—	—	14	13	9,2	8,6	16	15	18	17
Cyclops copépodites I—III	—	—	—	—	—	—	—	0,67	0,63	0,50	0,47	4,2	4,0	1,9	1,8
» » IV—V	—	—	—	0,15	0,14	—	—	—	—	—	—	1,1	1,0	0,50	0,47
Cyclops scutifer adultes	—	—	—	0,05	0,05	—	—	1,7	1,6	3,2	3,0	0,44	0,42	—	—
Daphnia long. hyal. ♀♀ jeunes	0,10			0,05		—		—		—		—		—	
» » » ♀♀ adultes	—	0,10	0,09	—	0,05	—	—	—	—	—	—	—	—	—	—
» ♂♂	—			—		—		—		—		—		—	
Bosmina coregoni	0,20	0,18	0,19	6,6	6,2	10	9,4	2,2	2,1	2,3	2,1	5,7	5,3	0,60	0,57
Polyphemus pediculus	—	—	—	0,05	0,05	—	—	—	—	—	—	—	—	—	—
Holopedium gibberum	—	—	—	—	—	—	—	—	—	0,33	0,31	11	10	2,0	1,9
Autres crustacés	—	—	—	—	—	—	—	—	—	—	—	0,11	0,10	0,10	0,09

tion G). Cependant les *Diaptomus* et les *Holopedium* sont emmenés en grand nombre du Stora Mjölkvattnet dans lequel ces espèces se trouvent probablement en plus grand nombre que dans le système des lacs de Vålån. Parmi les quatre séries de Mjölkvattnet, trois d'entre elles ont été prises à la vanne inférieure à la sortie du barrage du lac dont le niveau est réglé. A cet endroit l'effet de surprise est plus grand et les animaux évitent moins facilement la capture par les eaux de sortie. Il est difficile de poursuivre l'analyse par le fait du manque de station de comparaison dans les lacs d'où les animaux sont emmenés, ou plutôt à cause de la difficulté qu'il y a d'en choisir une (cf. Tabl. 9 et 10, op. cit. 1952). Tabl. 5 contient séries diurnes mais les variations dans l'abondance aux différentes heures sont aussi difficiles à interprêter. Du moins l'on peut dire que si une espèce ne déteste pas l'eau peu profonde de la zone littorale, elle remplira de ce fait une des premières conditions qui la porteront à être aspirée par le courant d'eau de déversement (cf. KOFOID 1908 p. 313). Ceci peut expliquer pourquoi les *Bosmina* sont assez nombreux dans les épreuves d'eau courante. De plus il a été démontré que les différentes formes de planctons peuvent être classées selon leurs possibilités à réagir par des mouvements de fuite lorsqu'elles sont mises en présence d'un tuyau qui aspire l'eau (NAUMANN 1921, WAUTIER 1949, LANGFORD 1953, ELSTER 1953). On a aussi montré qu'elles se laissent aller vers le fond lorsqu'il se produit des vibrations dans l'eau (EWALD 1910, STEUER 1910, avec bibliographie, ELSTER 1936). Ces réaction peuvent se manifester lorsque ces animaux se trouvent près d'un lieu de déversement ce qui diminue les chances de les voir emportés. BROOK et WOODWARD (1956) ont démontré que les naplii sont les moins agiles dans une lac — cf. Graph. 11. Enfin il faut compter sur le fait que les animaux peuvent être plus ou moins bien adaptés à subir le transport dans une eau courante. Un grand nombre de *Diaptomus* trouvés près de la vanne inférieur à Mjölkvattnet étaient déformés soit par l'effet de la diminution rapide de pression, soit parce que l'animal se déforme toujours dans l'eau courante rapide. Dans les affluents qui amènent l'eau dans les lacs et qui ont été étudiés, les *Bosmina* dominent, ce qui indique que ces animaux sont les mieux adaptés au transport par eau courante. KOFOID (1908) dit que les populations de *Cyclops* et *Bosmina* ont mieux survécu que la population de *Diaptomus* à une période de grand débit d'un fleuve et LILLJEBORG (1900) a souvent observé des *Bosmina* dans des eaux courantes.

La baie la plus isolée

Le Håckren (carte 2) comprend la baie de Fjällviken avec son bassin profond, la grande baie Nord-Est peu profonde et pauvre en planctons, le courant d'eau qui va de l'entrée à la sortie du lac traversant un bassin près de l'affluent, et la baie de Mankelviken dont il nous reste à caractériser la partie centrale.



Graphique 11. Les planctons crustacés des émissaires et des affluents, moyenne pour 5 l. V.i.=vanne inférieure, V.s.=vanne supérieure dans le lac réglé de Stora Mjölkvattnet. 24=série prise pendant 24 h. Légende comprise dans le graphique 10, △=Holopedium.

Selon l'analyse de NYBRANT qui se trouve dans la même publication, l'eau de Mankelviken se renouvelle très lentement par de l'eau apportée d'autres parties du lac. Ceci est très suggestif puisque c'est précisément dans cette baie que la densité de *Daphnia* atteint son maximum et par conséquent tous les planctons crustacés y atteignent leur maximum. Il est probable que la petite élévation de température en regard à celles prises à la même profondeur dans Fjällviken, n'a pas d'effet positif sur la biomasse des *Daphnia* et nous pensions que l'absence de courants d'eau est la raison la plus importante parmi celles que l'on puisse concevoir au sujet de cette richesse en *Daphnia*.

Compétition entre planctons filtrants

Dans plusieurs lacs d'Europe il existe deux espèces de *Bosmina* à l'intérieur du même lac, les *Bosmina coregoni* dans la région pélagiale et les *Bosmina*

Tableau 6. La température pour les épreuves des tabl. 1, 2, 4 et 5.

Lac	Date	Station	Profondeur	Temp. °C
Håckren	2.6.55	m 1—10	0	7 —10 3/4
			f	6 3/4— 8 1/2
	2.6.55	o	0	8 1/4
			f	8 1/4
	8.6.55	m 7—8	0	6 3/4
			f	6 3/4
	22.6.55	m 6—10	0	9 1/4—10 1/4
			f	8 1/4— 9 1/2
	3.7.55	m 6—10	0	11 1/2—12 3/4
			f	10 3/4—11 1/2
	10.8.55	k 1—5	0	15,1 —16,5
			f	14,5 —16,5
	10.8.55	n 1—5	0	14,6 —15,8
			f	13,8 —14,4
	11.8.55	g 1—5	0	11,8 —15,0
	11.8.55	i		11,4 —11,9
	11.8.55	h 1—5	0	14,4 —14,8
			2 m	14,2 —14,7
	13.8.55	D	1 m	15,4 —16,0
			2 m	15,1 —15,8
			f	13,9 —14,8
	13.8.55	f	0	16,4 —17,4
			f	15,8 —16,8
	13 et 15.8.55	E		15 1/4—16 1/2
St. Mjölkvattnet	3—4.8.55	V.i.		11
	6.9.56	V.i., V.s.		9

longirostris dans la région littorale. Cette dernière espèce existe aussi dans des étangs et dans de petits lacs (Schneider, 1908, Ter Porgossian, 1928, Aurich, 1933, Findenegg, 1953; cf. aussi Burckhardt, 1910 et Lieder, 1950). Cependant dans le nord de la Suède, Ekman a déjà signalé en 1904, la présence de *B. obtusirostris* (*B. coregoni obtusirostris*) dans la région littorale et dans la région pélagiale. Dans le matériel dont nous avons rendu-compte en 1952, et dans le nouveau matériel de Håckren, nous avons trouvé des *Bosmina coregoni* dans les deux régions sans pourtant pouvoir discuter à quelle race elles appartiennent (caractéristiques de l'espèce selon Burckhardt, 1941). Burckhardt (1910), Grover et Coker (1940), Tonolli (1949) et Lieder (1950) ont discuté des migrations obliques. Dans le matériel présent nous n'avons pas pu signaler de migrations diurnes obliques entre la région pélagiale et la région littorale. Par contre il y a une observation directe d'un essaim de *Bosmina* dans le Gesten qui se mouvait entre la région pélagiale et la région littorale (Nylén, manuscrit pas publié). De même un échange entre les populations de *Bosmina* dans ces deux régions dans le courant de l'été est très probable. Pour en trouver l'explication on peut sans doute songer à la végétation littorale moins dense des lacs du nord de la Suède en se référant aux suggestions faites par Burckhardt (1900, p. 177) pour les lacs Alpins. Dans des lacs où la végétation est plus riche on trouve dans la zone littorale plus d'animaux transitoires qui sont plus ou moins dependants des plantes ou du fond (STENROOS, 1898, ZACHARIAS 1898 a, STEUER 1901 et autres) et là aussi on trouve l'habitat des *Bosmina longirostris*.

Les planctons crustacés filtrants entrent en compétition, dans une certaine mesure, pour leur nourriture, même si la grandeur des pores de leurs filtres peuvent être un peu différents et même si la grandeur des pores n'est pas le seul facteur qui décide du choix de la nourriture (YOUNG 1928, COKER et HAYES 1940, RYTHER 1954, JØRGENSEN 1955). Nous considérons le fait que les *Daphnia* évitent les régions où la profondeur de l'eau ne dépasse pas trois mètres et que les *Bosmina coregoni* s'étendent sur la région littorale et sur la région pélagique, comme un effet des mécanismes qui tendraient à diminuer la compétition entre les espèces (cf. STEUER 1901 p. 54 et 138, ELTON 1929, HUTCHINSON 1951, RILEY 1953). Le dernier facteur qui régit la distribution des *Daphnia* peut être ou une réaction à la profondeur totale (BURCKHARDT 1910) ou une réaction à la lumière réfléchie du fond (LIEDER 1950) et il est peu probable que ce soit une effet du mouvement de l'eau puisque la limite entre la zone riche et la zone pauvre en *Daphnia* est distincte même par jours calmes (cf. RUTTNER 1930 p. 138). Les jours venteux une redistribution des animaux peut se produire (SOUTHERN et GARDINER 1926, p. 114) et il est probable que le mouvement des vagues sur l'eau peu profonde peut être dévastateur pour certaines espèces (BURCKHARDT 1900, p. 415).

Summary

The abundance of plankton crustacea was studied in different parts of a shallow lake. The samples were mainly taken in August, but the annual cycle is illustrated by some observations. The littoral plankton was dominated by *Bosmina* and *Polyphemus* at stations where the total depth did not exceed three metres. The depth distribution of *Bosmina* is discussed. The concentration of *Daphnia* in the central parts of the lake, two metres below the surface, ceased where the total depth was less than three metres. No diurnal migration between deep and shallow parts of the lake was observed, but it is assumed that *Bosmina* moves between these parts in the course of the summer. The plankton abundance was highest in a bay where the water is exchanged very slowly, and was very low in a part where the flow through the lake passes a shallow section. Plankton abundance in affluents and outlets from different lakes is described. The relation between variance and mean is discussed.

The theory necessary to explain the plankton distribution in the littoral region was already developed in many respects fifty years ago and cannot be greatly elaborated without further experiments. It includes reactions to depth (light) and currents, transportation by water movements and possible dependence on plants and bottom as substratum; also competition between filter-feeding crustacea. *Bosmina* can partly avoid the competition from other spe-

cies since its habitat includes streams and the most shallow parts of the littoral where other filter-feeding crustacea are rare. In northern Sweden *Bosmina coregoni* lives both in the littoral and the pelagial zone.

Index bibliographique

Apstein, C. 1896. Das Süsswasserplankton. Kiel, Leipzig.

Aurich, H. J. 1933. Das Zooplankton einiger Seen des Chiemgaus. *Int. Rev. 29: 295—345.*

Bainbridge, R. 1953. Studies on the interrelationships of zooplankton and phytoplankton. *J. Mar. Biol. Ass. U. K. 32: 385—447.*

Baldi, E. 1950. Phénomènes de microevolution dans les populations planctoniques d'eau douce. *Vierteljahrschr. Nat. forsch. Gesell. Zürich 95: 89—114.*

Barnes, H., Bagenal, T. B. 1951. A statistical study of variability in catch. *J. Mar. Biol. Ass. U. K. 29: 649—660.*

Barnes, H., Marshall, S. M. 1951. On the variability of replicate plankton samples. *J. Mar. Biol. Ass. U. K. 30: 233—263.*

Birge, E. A. 1895, 1897. Plankton studies on Lake Mendota. *Trans. Wiscons. Acad. Sci. 10: 421—484, 11: 274—448.*

Brehm, V. 1911. Beobachtungen über die Entstehung des Potamoplanktons. *Int. Rev. 4: 311—314.*

Brook, A. J., Woodward, W. B. 1956. Some observations on the effects of water inflow and outflow on the plankton of small lakes. *J. Anim. Ecol. 25: 22—35.*

Burckhardt, Annemarie. 1935. Die Ernährungsgrundlagen der Copepodenschwärme der Niederelbe. *Int. Rev. 32: 432—500.*

Burckhardt, G. 1900. Quantitative Studien über das Zooplankton des Vierwaldstädter Sees. *Mitt. Nat.-forsch. Gesell. Luzern: 129—437.*

— 1910. Hypothesen und Beobachtungen über die Bedeutung der vertikalen Planktonwanderung. *Int. Rev. 3: 156—172, 335—338.*

— 1941. Esistono forme intermedie fra «le due specie de Bosmina»? *Zeitschr. Hydrol. 9: 128—148.*

Coker, R. E., Hayes, W. J. 1940. Biological observations in mountain lake, Virginia. *Ecology 21: 192—198.*

Edmondson, W. T. 1955. The seasonal life history of Daphnia in an arctic lake. *Ecology 36: 439—455.*

Ekman, S. 1904. Die Phyllopoden, Cladoceren und freilebenden Copepoden der nord-schwedischen Hochgebirge. *Zool. Jahrb. Syst. 21: 1—170.*

Elster, H.-J. 1936. Einige biologische Beobachtungen an *Heterocope borealis. Int. Rev. 33: 357—433.*

— 1953. Einige Beiträge zur quantitativen Planktonmethodik. *Ber. Limnol. Flusstation, Freudenthal 4: 27—28.*

Elton, C. 1929. The ecological relationships of certain freshwater Copepods. *J. Ecol. 17: 383—391.*

Ewald, W. F. 1910. Ueber Orientierung, Lokomotion und Lichtreaktion einiger Cladoceren. *Biol. Centralbl. 30: 1—16, 49—63, 379—399.*

Findenegg, I. 1953. Kärtner Seen. *Carinthia 2: 1—160.*

Fisher, R. A. 1950. Statistical methods for research workers. London.

Francé, R. H. 1894. Zur Biologie des Planktons. *Biol. Centralbl. 14: 33—38.*

Fuhrmann, O. 1900. Beitrag zur Biologie des Neuenburger Sees. *Biol. Centralbl. 20: 85—96, 120—128.*

GROVER, W. W., COKER, R. E. 1940. A study on the depth distribution of certain net planksters in Mountain Lake, Virginia. *Ecology 21: 199—205.*

HUITFELDT KAAS, H. 1906. Planktonundersøgelser i Norske Vand. Christiania. Resumé.

HUTCHINSSON, E. 1951. Copepodology for the ornithologist. *Ecology 32: 571—577.*

JØRGENSEN, C. B. 1955. Quantitative aspects of filter feeding in evertebrates. *Biol. Rev. 30: 391—454.*

KOFOID, C. A. 1903, 1908. The plankton of the Illinois River. *Bull. Ill. State Lab. Nat. Hist. 6: 95—629, 8: 1—361.*

KOROTNEFF, A. 1904. Resultate d'une expédition zool. *Arch. Zool. Exp. Ser. 4. 12: 1—26.*

LANGFORD, R. R. 1938. Diurnal and seasonal changes in the distribution of the limnetic crustacea of lake Nipissing. *Univ. Toronto Studies, Biol. ser. 45 (LVI): 1—142.*

— 1953. Methods of plankton collection and a description of a new sampler. *J. Fish. Res. Bd. Canada 10: 238—252.*

LANGHANS, V. H. 1911. Der Grossteich bei Hirschberg. *Monogr. und Abh. Int. Rev. 3: 1—101.*

LIEDER, U. 1950. Beiträge zur Kenntnis des Genus Bosmina I. *Arch. Hydrobiol. 44: 77—122.*

LILLJEBORG, W. 1900. Cladocera Sueciae. Uppsala.

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

NAUMANN, E. 1921. Untersuchungen über das Verteilungsproblems limnischen Biosestons. *Kungl. Svenska Vetenskapsakad. Handl. 61: 1—28.*

NORDQUIST, H. 1921. Studien über das Teich-Zooplankton. *Lunds univ. Årsskrift N. F. 2, 17: 1—123.*

PENNAK, R. W. 1946. The dynamics of freshwater plankton populations. *Ecol. Monogr. 16: 339—355.*

REIF, C. 1939. The effect of stream conditions on lake plankton. *Trans. Amer. Micr. Soc. 58: 398—403.*

RICKER, W. E. 1938. On adequate sampling of the pelagic net plankton of a lake. *J. Fish. Res. Bd. Canada. 4: 19—32.*

RILEY, G. A. 1953. Theory of growth and competition in natural populations. *J. Fish. Res. Bd. Canada 10: 211—223.*

RUTTNER, F. 1930. Das Plankton des Lunzer Untersees. *Int. Rev. 23: 1—287.*

RYTHER, J. H. 1954. Inhibitory effects of phytoplankton upon the feeding of *Daphnia magna. Ecology 35: 522—532.*

SCHNEIDER, G. 1908. Der Obersee bei Reval. *Arch. Biontol. 2: 1—192.*

SCHRÖDER, B. 1898. Planktologische Mitteillungen. *Biol. Centralbl. 18: 525—535.*

SOUTHERN, R., GARDINER, A. C. 1926. The seasonal distribution of the Crustacea of the plankton in Lough Derg and the River Shannon. *Dep. Fish. Sci. Invest. Dublin 1: 1—170.*

STENROOS, K. E. 1895. Die Cladoceren der Umgebung von Helsingfors. *Acta. Soc. Fauna et Flora Fenn. 11: 1—45.*

— 1898. Das Tierleben im Nurmijärvisee. *Acta Soc. Fauna et Flora Fennica 17: 1—259.*

STEUER, A. 1901. Die Entomostraken fauna der «alten Donau» bei Wien. *Zool. Jahrb. Syst. 15: 1—156.*

— 1910. Planktonkunde. Leipzig, Berlin.

STRØM, K. M. 1926. Plankton from Finnmark Lakes. *Tromsø Mus. Årshefte 49: 1—23.*

TER-PORGHOSSIAN. 1928. Ueber die räumliche und zeitliche Verteilung von *Daphnia longispina* und *cucullata* sowie von *Bosmina coregoni* und *longirostris* im Klostersee bei Seeon. *Int. Rev. 20: 73—88.*

THOMASSON, K. 1952. Beiträge zur Kenntnis des Planktons einiger Seen im nordschwedischen Hochgebirge. *Schweiz. Zeitschr. Hydrol. 14: 257—288.*

TONOLLI, V. 1949. Ripartizione spaziale e migrazioni verticali della zooplankton. *Mem. Istit. Ital. Idrobiol. 5: 209—228.*

WAUTIER, J. 1949. Biocoenatique. *Bull. Mens. Soc. Linn. Lyon. 18: 76—80, 90—95.*
YOUNGE, C. M. 1928. Feeding mechanism in the invertebrates. *Biol. Rev. 3: 21—76.*
ZACHARIAS, E. 1893. *Forschungsber. biol. Station, Plön. 1: 1—52.*
— 1898. Das Potamoplankton. *Zool. Anz. 21: 41—48.*
— 1898 a. Das Heleoplankton. *Zool. Anz. 21.*
ZSCHOKKE, F. 1900. Die Tierwelt d. Hochgebirgseen. *Neue Denkschr. schweiz. Gesell. Naturw. 37: 1—400.*

Remarks concerning the flow through Lake Håckren

By G. NYBRANT

The Meteorological and hydrological institute of Sweden has performed temperature-measurements at several places in Lake Håckren, thereby measuring at different depths. These measurements were performed during the last two winters, when the lake was covered by an ice-sheet.

The lake forms two basins, a northern one and a southern one, separated by a shallow channel. Some isobaths are marked on a map, Fig. 1. The greatest depth in the northern basin is 10.9 m and in the southern one 17.1 m.

The temperature-values show that the water probably flows through the lake in the way marked on the map. The water in Mankelviken is exchanged very slowly by water coming from other parts of the lake. In Fjällviken, however, the water is exchanged rather quickly probably owing to secondary movements.

When the lake is ice-free, the flow through the lake is larger than during the winter. The exchange of water between the two bays — Mankelviken and Fjällviken — and other parts of the lake is as a rule probably the same as in winter. When strong winds are blowing, however, either from the east or from the west, these winds can in case the lake is ice-free cause surface currents so that the water is quickly exchanged also in Mankelviken.

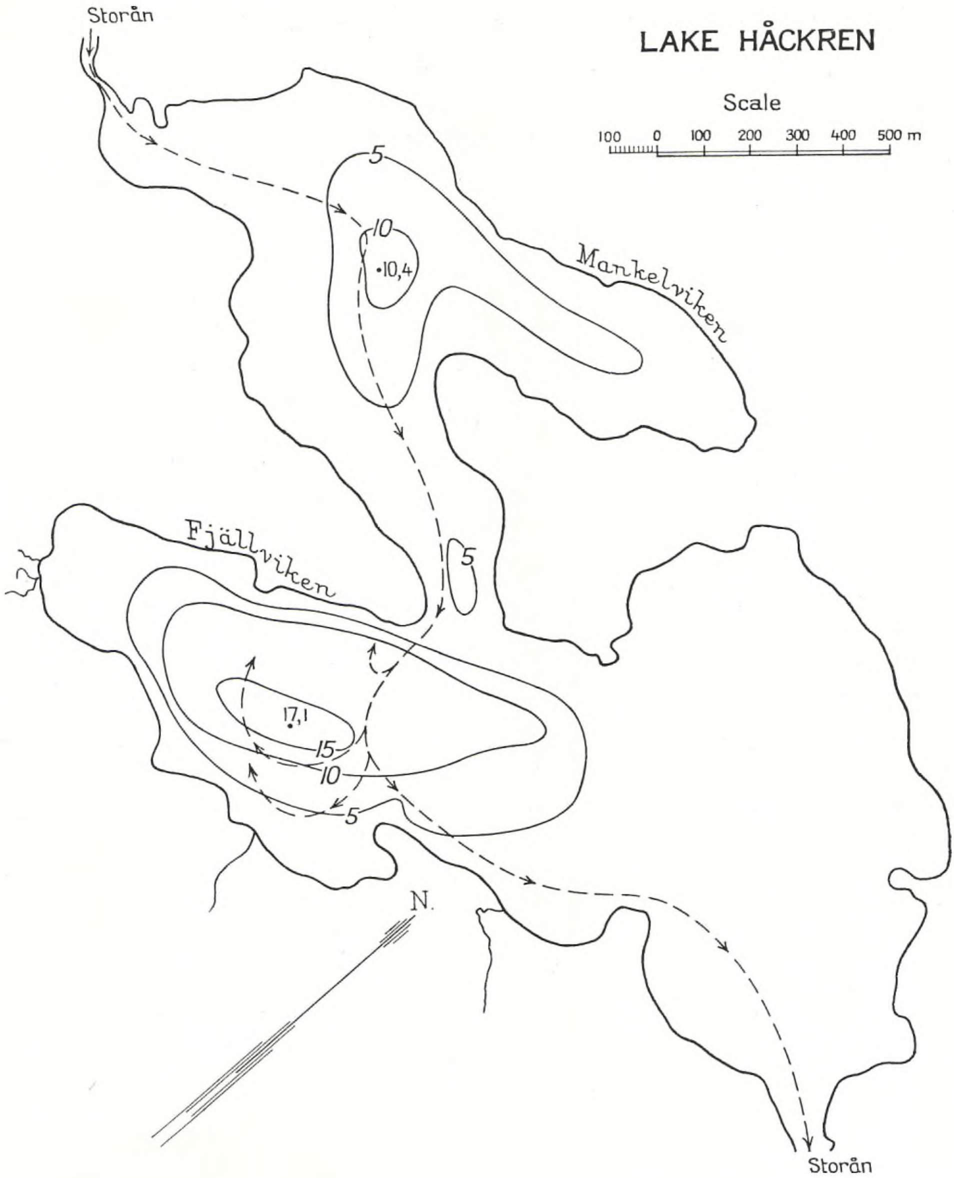


Fig. 1. Bathymetric chart of Lake Håckren. Contours at 5 m intervals. — — — main current.

On the Feeding Habits of Trout in a Stream of Northern Sweden

By Nils-Arvid Nilsson

1. Material and Methods

This paper is based on an investigation of the stomach contents of about 300 trout (*Salmo trutta* L.), fry (0) and older fish, in Lake Rensjön and in River Rensjöån in the district of Jämtland in northern Sweden during the years 1947, 1951, and 1955.

The fish were caught by gill-net fishing (in the lake and in the river sections with feeble current) and by electro fishing (in the river sections with strong current).

When calculating the share of the different items in the food of the fish a simple volumetric method was used (described in an earlier paper, Nilsson 1955). The percentage of every food item was calculated for every stomach, and the figures were used for the calculation of mean percentages of the compared fish populations.

As the fish population of a small stream like River Rensjöån is relatively small, and as there is a characteristic distribution of the different stages of the fish in the different parts of the stream (cf. Runnström 1957) the samples representing different stages or different parts of the stream must, as a consequence, be relatively small. This is the reason why not all fishing stations or all age groups have been compared from every point of view.

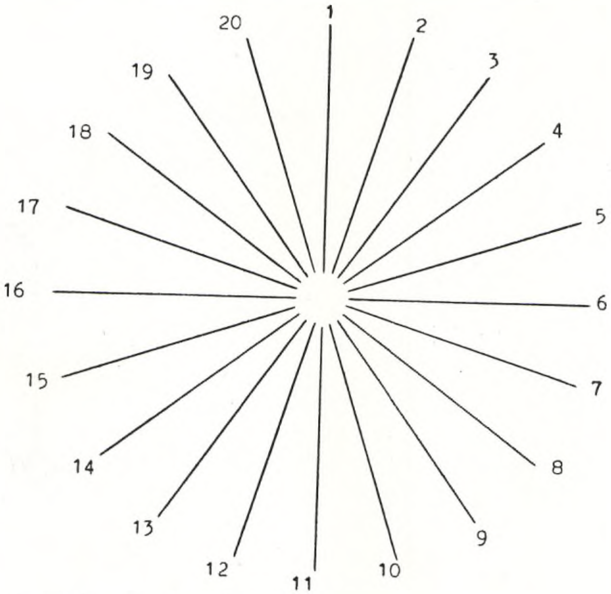
To illustrate diagrammatically the feeding habits of the fish under consideration the following method was used: The mean percentages given in table 3 were plotted in a radial diagram, were the perimeter represents 25 per cent and the points are bound together to display a characteristic figure (cf. Maucha's »Ionenfelderdiagram»). The food items were placed in the diagram after the principle presented at next page.

The age of the fish is marked »0» for the first summer after the birth, »I» for the second etc.

The investigation was carried out in cooperation with Dr. S. Runnström who organized the sampling, and dealt with the problems of growth, migration, and general population dynamics of the fish (cf. Runnström 1957).

2. The Area under Investigation

The geographical situation of the Lake Rensjön and River Rensjöån is shown on the map, Fig. 1. River Rensjöån runs through a mixed birch and



1. Vertebrates (Fi.=fish, Fr.=frogs).
2. Planktonic crustaceans (Ph.=*Phyllopoda*, Co.=*Copepoda*).
3. Semiplanktonic crustaceans (Eu.=*Eurycercus*).
4. Benthic crustaceans.
5. *Gastropoda* (Li.=*Limnaea*, Va.=*Valvata*, P.=*Planorbis*).
6. *Lamellibranchiata* (Pi.=*Pisidae*).
7. Other obligatory bottom animals (O.= *Oligochaeta*).
8. *Trichoptera* larvae (Tr. l.).
9. *Ephemeroptera* larvae (Eph. l.).
10. *Plecoptera* larvae (Pl. l.).
11. Aquatic *Coleoptera* larvae (Col. l.), *Megaloptera* larvae (Me. l.).
12. *Chironomidae* larvae (Ch. l.).
13. *Simuliidae* larvae (Si. l.).
14. *Tipulidae* larvae (Ti. l.).
15. *Trichoptera* pupae and imagines (Tr. p. i.).
16. *Ephemeroptera* imagines (Eph. i.), *Plecoptera* imagines (Pl. i.), *Megaloptera* imagines (Me. i.).
17. *Chironomidae* pupae and imagines (Ch. p. i.), *Simuliidae* pupae and imagines (Si. p. i.).
18. *Tipulidae* imagines (Ti. i.).
19. Terrestrial insects (T. I.).
20. Miscellaneous (Hy.=*Hydracarina*, No.=*Notonecta*).

pine forest. It falls from 500.9 to 493.0 m above the sea-level, and is characterized by a change between narrow sections with strong current (rapids) and broad sections with feeble current (pools, Swedish *hölja*). A regulation dam is built at the outflow of Lake Rensjön, but a fish ladder permits the migration of the fish from the river to the lake and vice versa. The fishing


NORWAY
RENSJÖAN
St. Rensjön
500.8
KALLSJÖN
380.8
Godön
Musvalen
Saxvallsklumpen
Dörrshöjderna
Skalsvallnet
Medstugusjön
536.0
Äggsjön
576.5
Häggsjön
436.8
Hästfjället
Sundsvalen
Trälhobnarna
Haraoarna
Mansbögarna
Anjeskutan
Varön
420.5
Grössjön
504
Kolhuset
Långön
Haranäset
Kamvallen fäb
Malnäset
Hvassnäs
Smedviken
Finnhögen
R.r. 170
R.r. 169 A
R.r. 169
R.r. 168
R.r. 167
Finnvåla
R.r. 166 A
R.r. 166
R.r. 165 B
R.r. 165 A
R.r. 165
R.r. 164 A
R.r. 164
R.r. 163 A

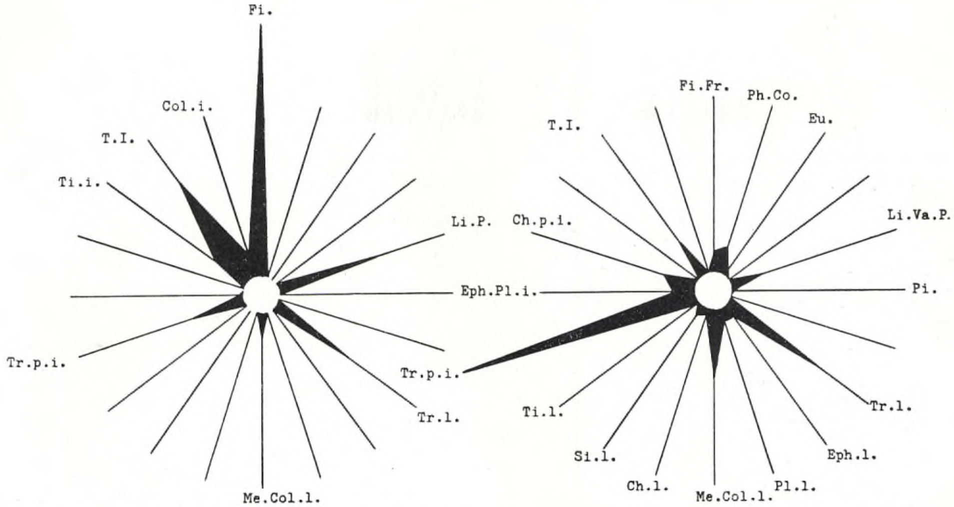


Fig. 2. The food of adult trout in Lake Rensjön (left) and River Rensjöån (right) in August 1955.

stations represent most of the types of habitats present in the river (cf. the diagram, Fig. 3).

Station 1 represents the fish ladder. All fish caught at this station were ascending.

Stations 2, 4, and 7 represent sections with strong current.

Stations 3, 5, 6, 8, and 9 represent sections with feeble current. The last two stations have the character of large ponds.

Stations 10 and 11 are not situated in River Rensjöån, but belong to the same drainage system, and have been included for comparison. They both represent river sections with strong current.

3. The Food of Adult[1] Trout

Investigations into the feeding habits of trout in the north Swedish mountain region have been carried out, amongst others, by MÜLLER (in running water, 1954 a, b) and NILSSON (in lakes, 1955). A characteristic trend, both in river- and lake-living trout, is an extensive consumption of *Trichoptera*-larvae during all seasons. An important category not present in lakes, but very characteristic in the food of the river-living trout is the so-called »organic drift» which occurs in all streams (cf. MÜLLER 1954 a, b, 1956, ROOS 1957). A comparison between the food of trout living in Lake Rensjön and River Rensjöån (diagram, Fig. 2) emphasizes above all the obvious importance of fish food (*Salmo* sp. and burbot) in the lake-living trout. This cer-

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[1] As adults have here been reckoned fish from age group III and older (for age distribution in Rensjöån cf. RUNNSTRÖM 1957).

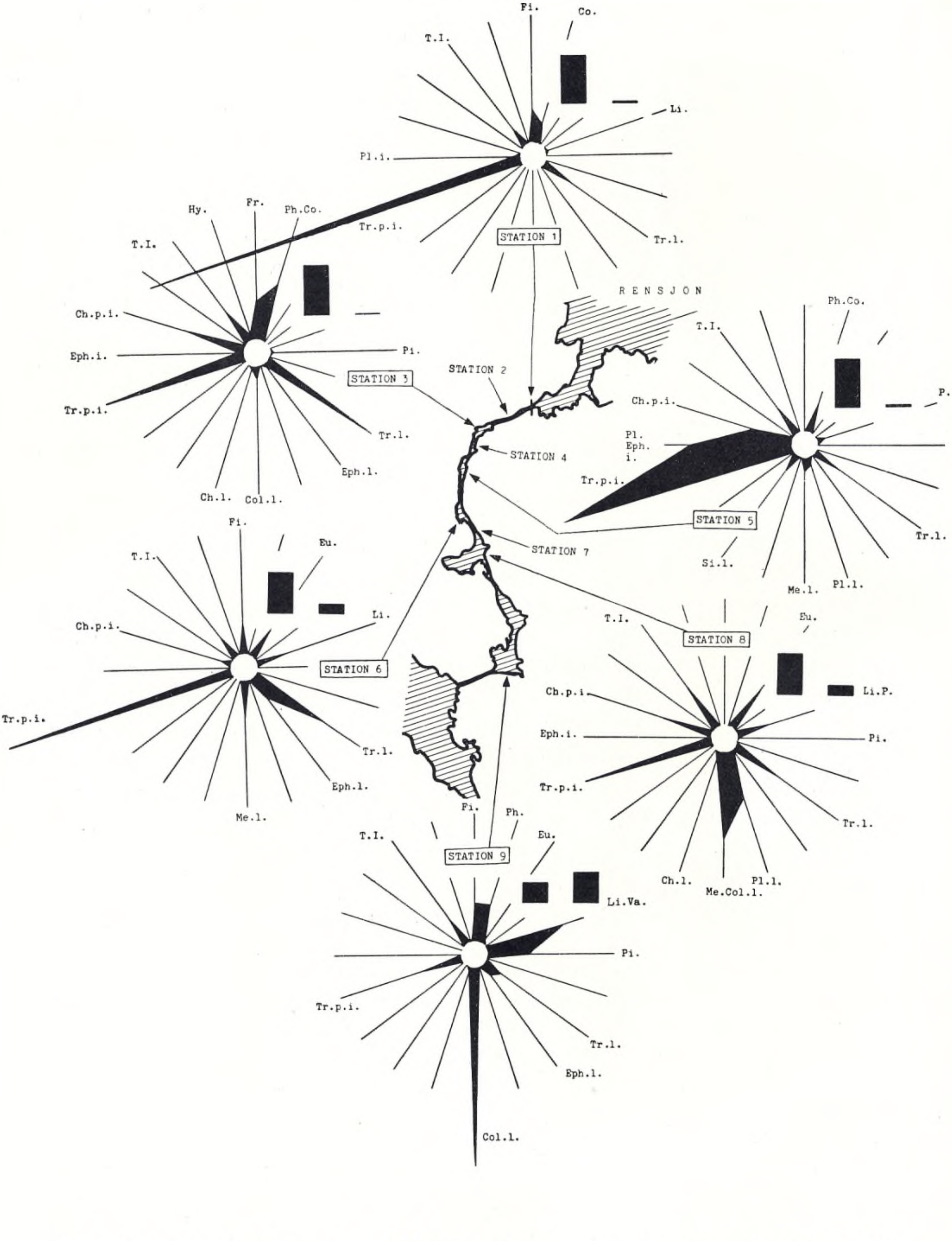

Fig. 3. The food of adult trout at 6 different fishing stations in River Rensjöån during August 1955. The piles represent the ratio obligatory drift animals (left): obligatory bottom animals (right).

Table 1. The consumption of pure drift food. (*Phyllopoda, Copepoda, Trichoptera* p., *Chironomidae* p. and terrestrial insects) and of pure bottom food (*Limnaea, Valvata, Planorbis,* and *Pisidae*) by trout at 6 different fishing stations in River Rensjöån.

Fishing station	Drift food, mean percentage	Bottom food, mean percentage	Ratio drift : bottom food
1	8.0	0.6	93 : 7
3	38.5	0.7	98 : 2
5	28.9	1.5	95 : 5
6	31.3	6.7	82 : 18
8	27.9	6.6	81 : 19
9	14.7	23.8	38 : 62

tainly depends on the much greater average size of the trout in the lake compared with that in the river permitting them to consume as big food objects as other fish. It may also be observed that planktonic crustaceans are fully lacking in the food of the lake-living trout (cf. also NILSSON 1955).

The organic drift and its importance in the biological productivity has been treated, amongst others, by MÜLLER (1954 a, b, 1956) and ROOS (1957). It has been shown that in the stream itself there is a continuous drift of benthic animals. Its biological significance has been suggested to consist in a colonization mechanism implying an up-stream migration of imagines and a resulting superabundance in the upper parts of the streams which in its turn is levelled by the drift: »colonization cycle» (MÜLLER 1954 b). To the drift may also be reckoned pupae and imagines of the aquatic insects as well as terrestrial insects floated along by the stream. Moreover, in rivers originating in lakes there is also a drift of purely limnic organisms, above all planktonic crustaceans who have been carried out by the current in the outflow of the lake. MÜLLER (1956) showed that in september the bottom fauna of the upper part of the river Åreälven in northern Jämtland was about 13 times more abundant than in the lower part, the drift about 24 times more abundant.

The diagram, Fig. 3, illustrates the food of the trout at 6 different fishing stations in River Rensjöån during August 1955. It is obvious that there exists a significant change of food objects between the upper and the lower parts of the stream, station 1 showing a very marked predominance of imagines of *Trichoptera,* station 9 of larvae of *Dytiscidae.* In spite of the fact that this phenomenon may be caused by several factors, e.g. differences in the fauna of different parts of the stream resulting from differences in the rapidity of the water, differences in the average size of the fish in different parts of the stream (cf. RUNNSTRÖM 1957, p. 204) which in its turn always means differences in feeding habits etc., it seems, nevertheless very probable that the differences in the abundance of the organic drift mentioned above play the most important part. If we distinguish between the food objects appear-

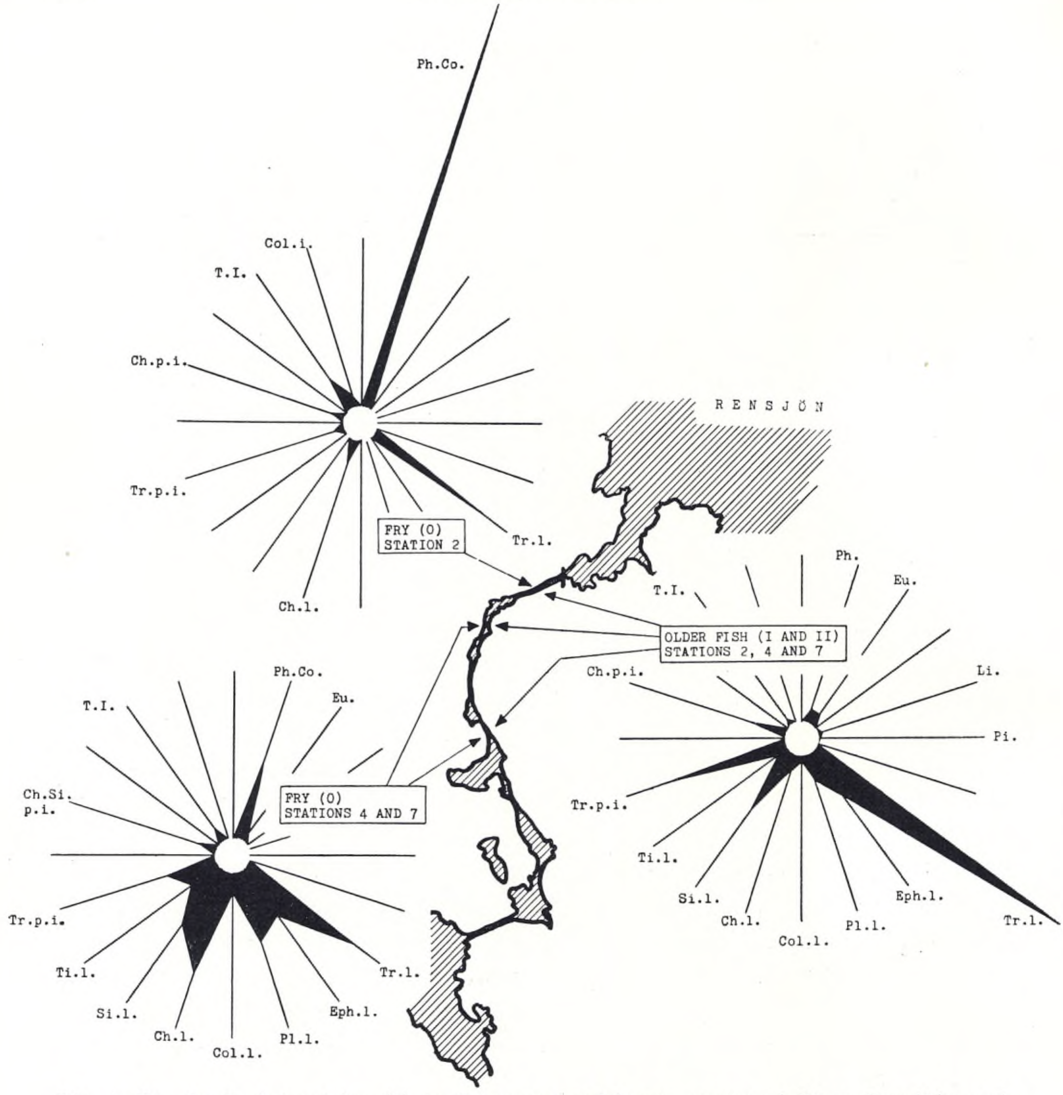

Fig. 4. The food of trout fry (0) in the upper and lower course of River Rensjöån and the food of older fish (I and II) at the same stations in August 1955.

ing exclusively or almost exclusively as drift or bottom food in a stream (*Phyllopoda, Copepoda Trichoptera* p., *Chironomidae* p. and the terrestrial insects representing the obligatory drift animals, *Limnaea, Valvata, Planorbis,* and *Pisidae,* representing the obligatory bottom animals), and examine their occurrence in the food of the trout at the different fishing stations we obtain Table 1.

Although the obtained ratio between drift food and bottom food does of course not represent the true relation the tendency of an increasing import-

Table 2. The position of planctonic crustaceans consumed by trout fry in River Rensjöån. Calculated as percentages of fish examined.

	July 1955	Aug. 1951	Aug. 1955	Sept. 1947	Sept. 1951
Eurycercus			3		
Daphnia	13	9	12	43	33
Bosmina	75		8		
Holopedium		34	19	36	33
Bythotrephes		35	35		
Heterocope		22	23	21	
Cyclops	12				33

ance of drift food in the upper reaches of the river seems obvious. The same tendency can be discerned in the feeding habits of the fry, though in a still more marked way (cf. the diagram, Fig. 4).

Whether appearing as drift or bottom food the most important part in the food of the trout is played by the *Trichoptera,* belonging mostly to the genera *Plectrocnemia, Sericostoma, Hydropsyche, Wormaldia,* and *Agrypnia.* Larvae of *Agrypnia obsoleta* (det. T. ROOS) characterize above all the food of trout of the lake and the ponds.

4. The Food of the Fry

All fry were caught in strong current at the stations 2, 4, and 6. On comparing the food of the fry with the food of the somewhat older fish (I and II) from the same stations (diagram, Fig. 4) we find the taxonomic composition of the food objects to be rather similar. An important difference seems, however, to lie in a much greater consumption of planktonic crustaceans by the fry. As mentioned above this tendency seems strongest in the upper course of the river. On the whole the fry consume much smaller food objects: the *Trichoptera*-larvae, for example, eaten by the fry, as though belonging to the same genera as those eaten by the older fish, represent much earlier and smaller stages. It seems likely that this illustrates a general rule concerning the food consumption of all fish (cf. e.g. LINDSTRÖM 1955, NILSSON 1955).

The seasonal variations in the feeding habits of the fry (diagram, Fig. 5) are a function of the seasonal variations in the abundance in the fauna of the stream, available to the fish. In June exists a very marked predominance of chironomid-larvae (mostly of the genera *Ablabesmyia* and *Psectrocladius*). In the course of the summer, however, the importance of the organic drift (mostly planktonic crustaceans) increases. Table 2 illustrates the taxonomic position of planktonic crustaceans consumed by the fry during the different seasons and years under consideration.

A well-known trend in the feeding behaviour of the salmonid fishes is

Table 3. The food of trout and

	Trout							
	Older fish							
	% Lake Rensjön, Aug. 1955	% Migrating fish Station 1, Aug. 1955	% Strong stream,(I and II) Station 2, 4, 7 Aug. 1955	Slow stream, Aug. 1955				
				Stations				
				3 %	5 %	6 %	8 %	9 %
Vertebrates								
Frogs				7.7				
Fish	35.3	6.7				5.8		7.3
Organic drift (in running water)								
Phyllopoda			4.4	6.2		6.7	9.5	8.5
Copepoda		4.0		5.4	5.8			
Trichoptera i.	7.3	76.7	17.8	18.5	33.1	28.3	20.9	7.7
Trichoptera p.				10.0	13.1	17.9	5.2	
Ephemeroptera i.				1.5	8.5		0.3	
Plecoptera i.	0.7	1.3			11.2			
Chironomidæ i.			1.4	3.1	1.5	0.4	5.6	
Chironomidæ p.			1.1	9.6	3.8	1.7	4.2	
Simuliidæ i.				0.7	2.7			
Tipulidæ i.	5.3							
Terr. insects	17.0	4.0	1.1	7.3	6.2	5.0	9.0	6.2
Actively swimming								
Dytiscidæ i.	3.3							
Notonecta								
Hydracarina				0.7				
Bottom animals								
Oligocheta								
Limnæe	6.7	0.6	0.6			6.7	2.5	3.8
Valvata								12.3
Planorbis	8.0				1.5		3.8	
Pisidium			0.3	0.7			0.3	7.7
Trichoptera l.	12.7	6.7	45.3	23.5	5.4	15.8	10.4	4.2
Ephemeroptera l.			8.1	1.2		4.6	0.3	2.7
Plecoptera l.			3.9		1.5		9.6	
Sialis l.	3.0				2.3	7,1	4.2	
Dytiscidæ l.	0.7			2.7			12.7	38.8
Helmidæ l.			0.8					
Chironomidæ l.			2.5	1.2			1.3	0.8
Simuliidæ l.			10.8		3.5			
Tipulidæ l.			1.9					
Percentage sum	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Empty stomachs	0.0	59.5	0.0	0.0	7.1	7.7	0.0	13.3
Number of specimen examined	15	37	17	13	14	13	29	15
	153							

burbot in the River Rensjöå-district

									Burbot	
Fry (0)							Older	Fry (0)	Older	Fry (0)
Station 2						Station 4, 7, Aug. 1955	River Rödingbäcken Station 10, Aug. 1955	River Lakavattenbäcken Station 11, Aug. 1955	All stations, Aug. 1955	All stations, Aug. 1955
% June 1947	% Sept. 1947	% Aug. 1951	% Sept. 1951	% July 1955	% Aug. 1955	%	%	%	%	%
									15.0	
	56.5	42.1	9.3	16.9	34.7	6.1				
	10.5	28.2	3.6	1.1	28.9	7.0			8.3	
	2.5		6.4	13.1	2.3	5.7	44.4			
						2.3				
			6.4							
		0.5		8.3	1.8	2.5	2.5			
15.4		3.2		6.1	1.6			1.4		
						0.6				
2.5		2.0	1.4		5.5	2.3	0.6			
	7.5				1.8					
			7.9							
2.5	14.5	3.4	5.0	22.8	20.0	19.8	30.6	30.7	50.0	40.0
	3.0	3.7	36.4			8.4		47.1	8.3	22.9
	5.5	1.6	17.9			10.9	15.0		15.4	37.1
						3.0				
79.6		13.7	5.7	8.9	3.4	16.1	2.5	20.7	3.0	
		1.6		17.2		10.5	4.4			
				5.6		4.8				
100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
0.0	9.1	0.0	0.0	0.0	4.3	0.0	0.0	0.0	14.3	25.0
12	11	19	7	18	23	22	8	7	14	9
127									23	

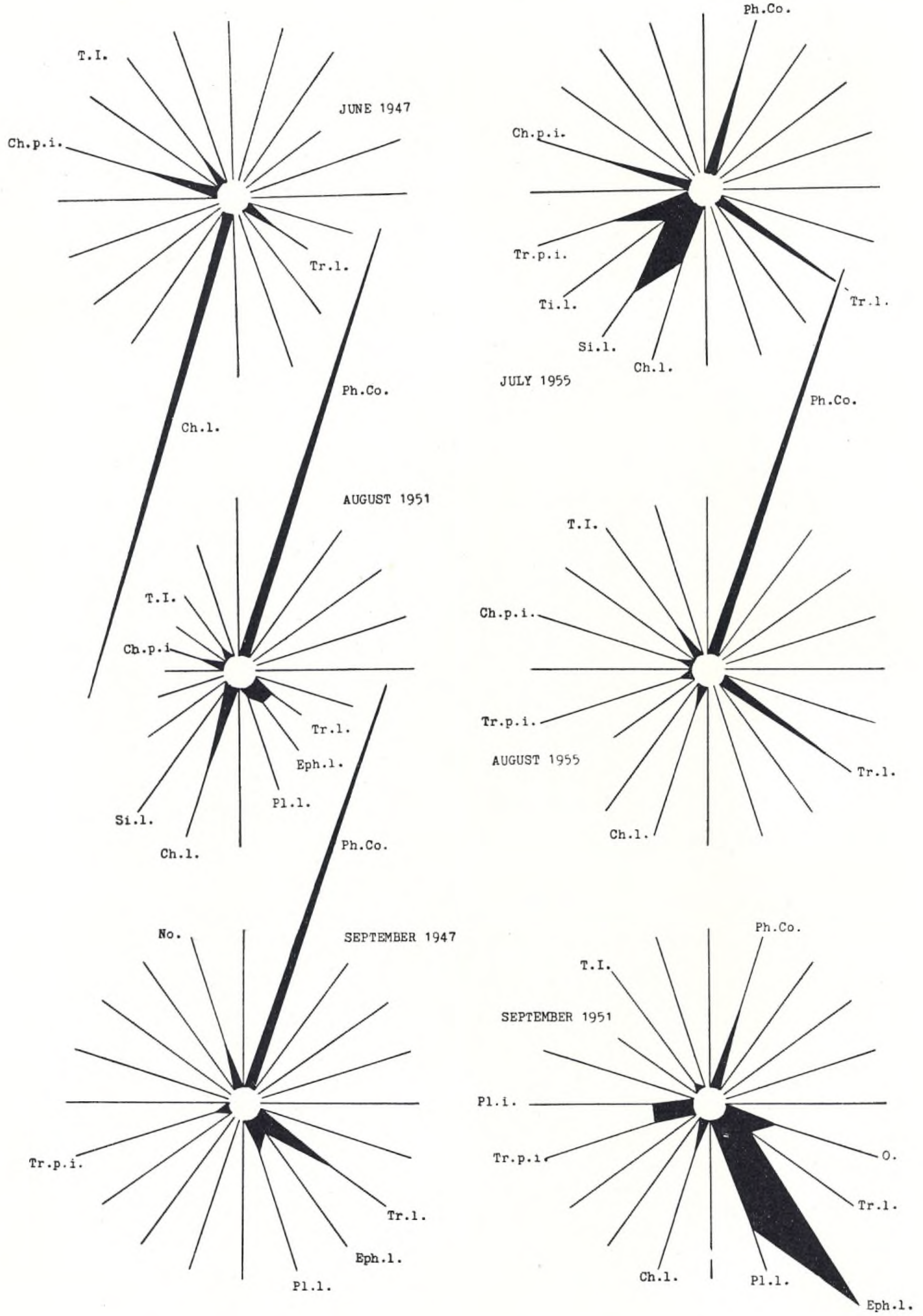

Fig. 5. The food of trout fry in River Rensjöån (fishing station 2) during some different seasons and years.

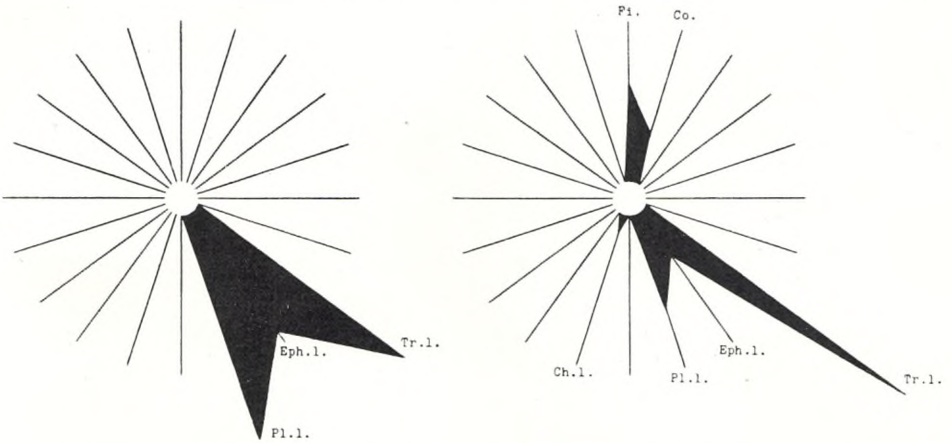

Fig. 6. The food of burbot, fry (left) and older fish (right) in River Rensjöån during August 1955.

the obvious tendency to become adapted to a certain food object when this object reaches an abundance that makes it more available to the fish species in question than any other food object occurring in the fauna at that time (cf. Lindström 1955, Nilsson 1955). This phenomenon appears to the examiner of the stomachs as an obvious dominance of certain food objects: often every stomach is filled with a specific food object. It is now of fundamental interest that this tendency seems very weak or altogether lacking in the younger stages of the trout. Lindström (1955) observed that fry of char reacted only to moving objects, also very big ones (e.g. fry of pike). The present author and Dr E. Fabricius have also observed that in aquaria fry of char react to any moving particle by snapping. Non-edible particles, however, were immediately sput out. This indicates that the behaviour mechanism regulating the feeding of the younger stages of the fish is of a basic type, much simpler than the corresponding mechanism in the adult fish.

5. The Food of Burbot in a Trout Stream

A small material of burbot (*Lota lota* L.) was sampled in connection with the catching of trout. All burbot were of very small size, the biggest adult specimen reaching 160 mm. A comparison between the food of the burbot and the food of the trout of River Rensjöån (diagram, Fig. 6) shows that they share their main bottom food, larvae of *Trichoptera*. This could be interpreted as indicative of severe competition between the two species. The fact, however, that burbot do not seem to use the drift food to any important extent may indicate that, in streams as well as in lakes, they are pure bottom feeders, possessing a niche different from the niche of trout which in running water feed mainly on drift (cf. also MÜLLER 1954). Much more material is, however necessary for the solving of the problem of competition between trout and burbot.

All fish consumed by the burbot consisted of its own fry.

6. Summary

1. The stomach contents of about 300 trout, adults and fry, from the River Rensjöån district in northern Jämtland were examined.

2. Differences were found in the food of lake-dwelling and river-dwelling trout, the lake-dwelling trout feeding mainly on fish and insects, the river-dwelling mainly on organic drift.

3. Differences were found in the consumption of the food in the upper and in the lower course of the stream, the part played by the organic drift being more important in the upper course.

4. The fry were found to consume mainly food objects of smaller size than the adults, mostly planctonic crustaceans carried out by the current in the outflow of the lake.

5. The behaviour mechanism regulating the feeding of the fry is supposed to be of a simpler, more basic type than that of the adult fish.

6. Burbot were found to share their main bottom food, larvae of *Trichoptera,* with the trout. They did not, however, consume drift food to any important extent.

Literature

LINDSTRÖM, T. 1955. On the relation fish size — food size. *Rept. Inst. Freshw. Res. Drottningholm 36: 133—147.*

MAUCHA, R. 1932. Hydrochemische Methoden in der Limnologie. Binnengewässer 12. Stuttgart.

MÜLLER, K. 1954 a. Produktionsbiologische Untersuchungen in Nordschwedischen Fliessgewässern. Teil: 2. Untersuchungen über Verbreitung, Bestandsdichte, Wachstum und Ernährung der Fische der Nordschwedischen Waldregion. *Rept. Inst. Freshw. Res. Drottningholm* 35: 149—183.

— 1954 b. Investigations on the organic drift in north Swedish streams. Ibid. 133—148.

— 1956. Das produktionsbiologische Zusammenspiel zwischen See und Fluss. *Ber. Limn. Flusst. Freudenthal VII: 1—8.*

NILSSON, N.-A. 1955. Studies on the feeding habits of trout and char in north Swedish lakes. *Rept. Inst. Freshw. Res. Drottningholm 36: 163—225.*

ROOS, T. 1957. Studies on upstream migration in adult stream-dwelling insects. I. *Rept. Inst. Freshw. Res. Drottningholm 38: 167—193.*

RUNNSTRÖM, S. 1957. Migration, age and growth of the brown trout (*Salmo trutta* L.) in Lake Rensjön. *Rept. Inst. Freshw. Res. Drottningholm 38: 194—246.*

Studies on Upstream Migration in Adult Stream-Dwelling Insects. I

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Contents

I. Introduction

It is a well known phenomenon that aquatic organisms occur drifting in running water. Lake-plankters as well as benthic organisms from lake-outlets and streams are now and then swept by the current away from their habitual environments, and transported downstream for some distance.

Some observations on this stream drift were reported by Woltereck (1908), referring to planktonic lake algae, and by Borgh (1927, unpublished), referring to benthic stream animals. Later on comprehensive investigations into stream drift and restocking of denuded situations appeared. Needham (1928 a), Ide (1942), Dendy (1944), Wolf (1947), Knöpp (1952), and Müller (1954 a) have shown stream drift to be a normal feature even in the absence of floods. Dendy found that in one stream all species represented in bottom-fauna samples occurred sooner or later in the drift of this stream. MÜLLER obtained similar results. At times of flood portions of certain creek bottoms can be almost depopulated by the strong current, and the injury to and the mortality among drifting animals is very considerable (NEEDHAM 1929, BEAUCHAMP 1932, CHANDLER 1937). However, MOFFETT (1936), LEONARD (1942), and MÜLLER (1954 a) have shown that eroded areas and newly excavated stream-channel diversions are rapidly restocked. The invading animals proved to have drifted into the areas from higher up, either as eggs or as nymphs and larvae.

Pools and lakes serve as catching basins for animals in stream drift (NEEDHAM 1930, BEAUCHAMP 1932, DENDY 1944). These animals survive in the new environments but for a limited time, succumbing to wave action, silt deposition, and unsuitable temperature (BEAUCHAMP 1932, DENDY 1944).

The magnitude of the drift in lake-outlets has recently been studied by KRIEGSMANN (1952) and GEISLER (1953), while MÜLLER (1954 a, 1954 b, 1955, 1956) has elucidated the problem in streams. They all have shown that considerable quantities of biological material are transported downstream as organic drift. The term »organic drift» was introduced by MÜLLER (1954 a), who has thoroughly studied the problem in Sweden.

Thus the activity of the current produces upon the lotic fauna among other things the effects of depopulation, distribution, and restocking. As these are working in the direction of the current the inhabitants of a stream would gradually be transported downstream, and at last succumb in unsuitable environments. Consequently there must exist some mechanisms, which compensate the losses, and ensure a balance and the retention of the population. The positive rheotaxis of torrential organisms has been suggested as such a compensating factor. By marking nymphs and making frequent collections HARKER (1953 b) has shown that the nymphs of *Ecdyonurus torrentis* KIMM. (*Ephem.*) migrate upstream during November. MACAN (1957) found the new generation of *Rhitrogena semicolorata* CURT. and *E. torrentis* (*Ephem.*) to be most abundant at a point higher upstream than the old generation. This could be due to upstream movements of adults before oviposition or of nymphs after the eggs had hatched, but on this no observations were made.

Indeed, the positive rheotaxis produces a certain effect, but can not be fully adequate as a compensation for the population losses through drift (cf. MÜLLER 1954 a).

Of far greater importance as a compensating factor is an upstream movement for oviposition, accomplished by the adult stream-dwelling insects. Literature does not report any special investigations on this phenomenon, but brings only sporadic observations, in most cases concerning *Ephemerop-*

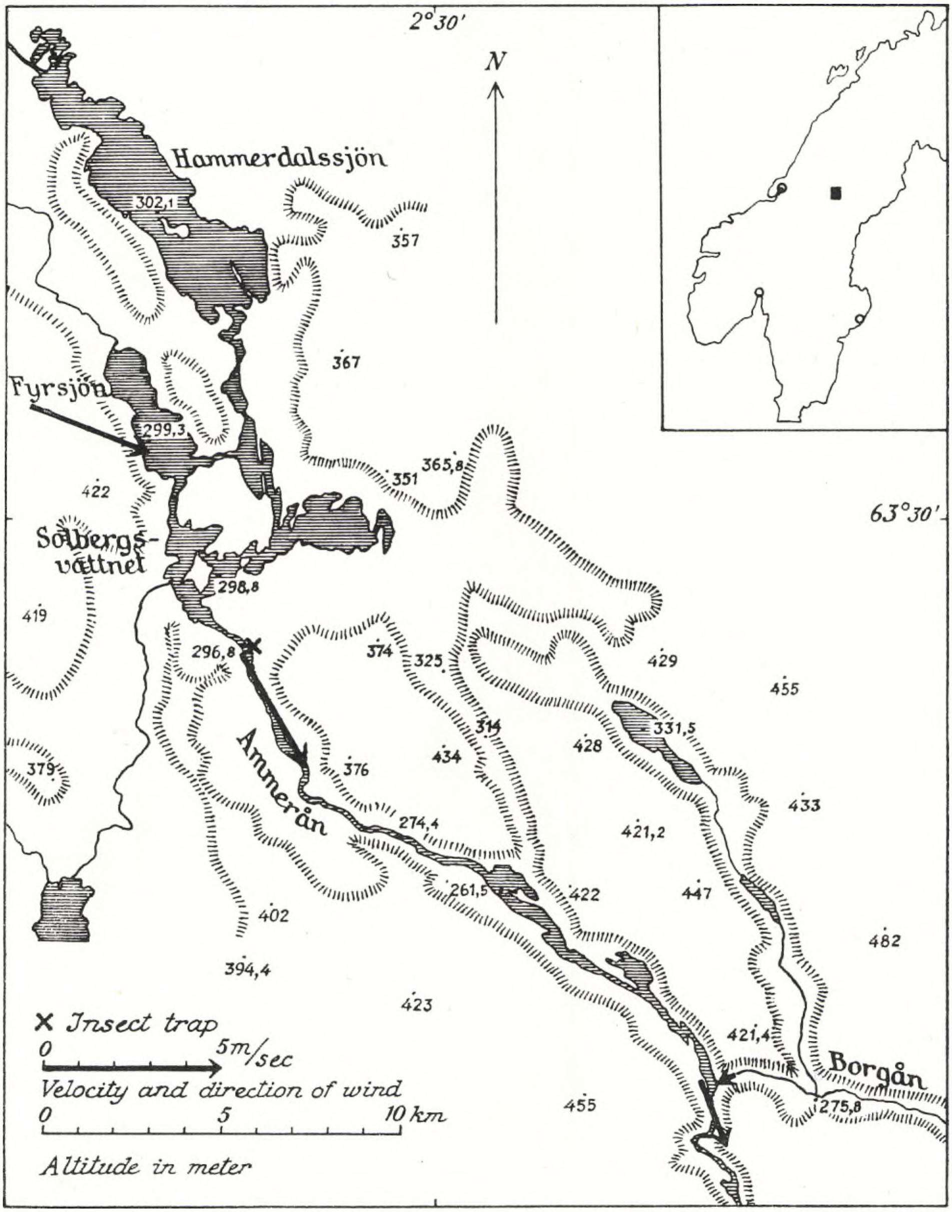

Fig. 1. Map of the investigated area showing geographical situation, localities, and topography, also wind conditions on Aug. 28th 1956.

tera. Thus STADLER (in ULMER 1927) and SCHÖNEMUND (1930) report *Polymitarcis virgo* OLIV. and *Caenis macrura* STEPH. (=*halterata* FABR.) (*Ephem.*) respectively, as flying in swarms upstream for kilometres. SAWYER (1950) states *Ephemerella ignita* PODA to fly upstream before oviposition. HARRIS (1952) adduces several examples among *Ephemeroptera* (*E. ignita, E. notata* EAT., *Siphlonurus* sp.) and *Trichoptera* (*Hydropsyche* spp.). According to him the females of these insects fly upstream until fast-flowing or broken water is reached, where they approach the water surface, and drop their eggs. He considers the phenomenon as valid for most ephemeropterans. MÜLLER (1954 a) noticed a distinct accumulation of the imagines of *Simuliidae* in the upper reaches of streams, in which the juvenile stages were distributed all through the course. He postulates a general upstream migration of the imagines of lotic insects, and puts this in connection with the organic drift. The term *colonization cycle* is proposed by him for the total phenomenon of organic drift — upstream migration.

The aim of this paper is to elucidate and prove this upstream migration. Mere watching of the cloud of swarming insects over a rapid in a lowland-river produces a strong impression of a predominantly upstream flight-direction. This I found quite obvious in big and easily recognizable insects, such as *Sericostoma personatum* SPENCE (*Trich.*) and *Ephemera danica* MÜLL. (*Ephem.*). It was, however, necessary to find a method as objective as possible for the sampling of swarming insects.

II. The investigated locality

The investigations were carried out on *River Ammerån* in the province of Jämtland, Northern Sweden, cf. Fig. 1. The Ammerån is a tributary to the River Indalsälven. The investigated locality is situated in Hammerdal parish, and includes Lake Solbergsvattnet, its outlet, and a section of rapids in the Ammerån below the outlet. Lake Solbergsvattnet is situated on the sub-Cambrian peneplane just east of the Cambro-Silurian table-land with 100—130 m greater altitude. It is a lake of throughflow with a gradient of 0.1 m per km, not enough for producing noticeable current phenomena upon the surface. The maximal depth is 15 m, and the lake-type is eutrophic with vast belts of reeds and on the whole a rich flora. Bare surf-shores are very scarce. The River Ammerån runs in a marked valley, about 1 km broad and 50—70 m deep, with spruce- or pine-forests and mires on the slopes. The longitudinal gradient is 5.7 m per km in the investigated section. The river-bed consists of rubble and gravel with large moraine-boulders. Alder-trees, birches, and willows line the banks, further off grow tall conifers. Owing to great variations in water-level during the summer the width of the river ranges from 80 m at high water to 45 m at low water. When the samples were taken the width was 75 m (1953) and 55 m (1955), leaving an open gravel-shore of 3—6, and 10—12 m, respectively, between the forest on the bank and the water-line.

III. Methods and definitions

Environmental conditions. Air-temperature and relative humidity were recorded by means of a modern thermo-hygrograph (Lambrecht No. 252) placed mid-stream in a thermometer-case 1.5 m above the surface of the water. The wind-velocity was estimated (in degrees Beaufort), gauged by an anemometer (Dr. Östman's anemometer) or by a pitot tube (Lambrecht No. 640). The surface velocity of the water current was gauged by a mechanical velocity meter.

Preparatory experiments, net-catching. In 1953 I made some preparatory experiments by simply catching insects, flying over the surface of the water. This was done from a point in the river by means of an ordinary insect net, 33 cm in diameter and with a 100 cm long handle. I first caught for 20 minutes specimens flying upstream, then turned round, and caught downstream flying insects for the same period (July 2nd). Later on I caught alternately from either direction for 5 minutes, altogether for half an hour (July 10th).

Main experiments, the insect trap. In 1955 I used an insect trap in order to get a more extensive, objective material. The trap is a modification of Malaise's bilateral insect trap (MALAISE 1937). The alteration implies the keeping apart of the catches from the two opposite halves of the trap by means of a vertical partition wall, cf. Fig. 2. Briefly, each trap-half consists of a parallelepiped of bobbinet, 300×180×180 cm, with one side missing so as to provide an inlet. The ceiling is raised obliquely towards one of the hind corners, where a square opening with 15 cm side opens into the upper compartment. The latter has the form of an oblique pyramid with an upturned netting-funnel in the middle. The apex of the pyramid is fastened to a brass tube which leads into a killing cylinder made of sheet-metal. This has three compartments, the upper two of which are soldered together, and have funnel-shaped floors with a hole at the bottom. The uppermost compartment has a window covered with brass netting opposite the entrance tube, protected against rain by a projecting plate roof. The lowermost, removable compartment has flat bottom, and acts as anaesthesia chamber. As anaesthetic acetic ether is used. The ether vapour is furnished by a little bottle with a wick through the cork, and which is suspended from the bottom of the middle compartment. The trap is made of black bobbinet, and all borders are strengthened by cottonbands and provided with loops for erection. The

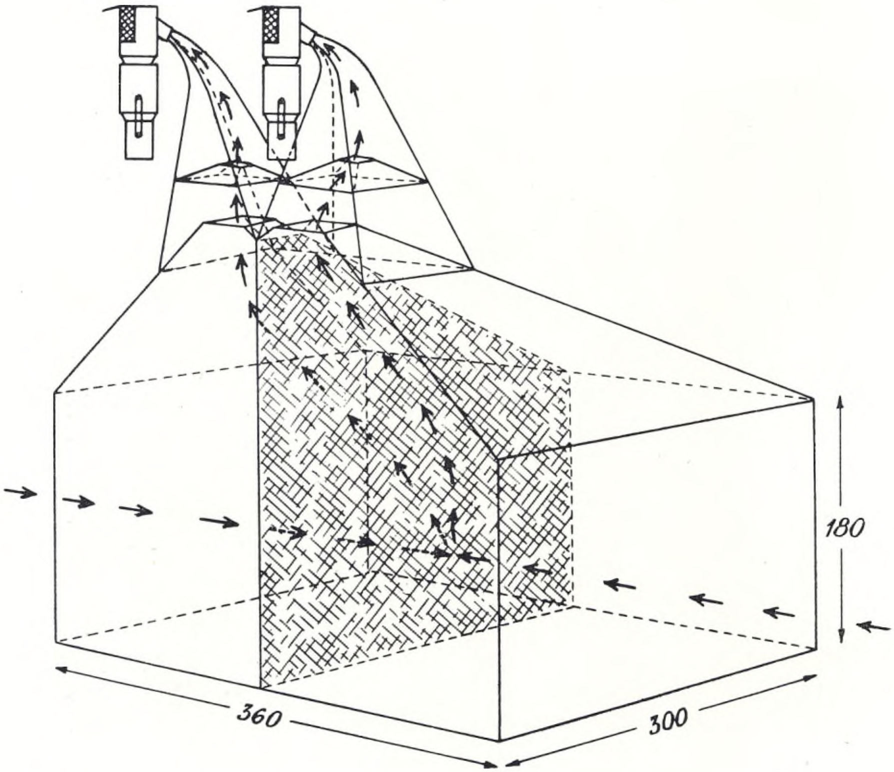

Fig. 2. Perspective sketch of the insect trap. The arrows indicate the way of the captured insects in the two halves of the trap. Measurements in cm. For explanation, see text.

bottom of the trap is made of a light and cheep cotton fabric. Compare moreover the sketch, Fig. 2.

The insect trap was erected by means of stakes and streched ropes at the same little point, where the preparatory experiments had been carried out. It was placed entirely out over the water with the bottom 20 cm above the surface of the water and the long sides parallel to the river course, i.e. with one entrance directed upstream and the other downstream, cf. Fig. 3. A 12 m wide open shore with gravel separated the trap from the forest upon the bank. The anaesthesia cylinders were examined and emptied several times during the experiments, for the last time after 36 (sample 3), and 41 hours (sample 4). The trap was then taken down, and placed in a box in acetic vapour, whereupon remaining insects could be collected.

Even these methods are not perfect. The insect trap, especially its edges and stage, forms an obstacle which is to some degree avoided by certain insects, but which attracts others (for oviposition). Some few decimetres from the edges, however, most insects keep straight on with unaltered speed.

Fig. 3. The insect trap set in River Ammerån. The trap is of smaller size than that referred to. The locality is the uppermost rapid at the outflow from Lake Solbergsvattnet.

Moreover, the repellent or attractive action is relatively equal for both halves of the trap, as is also the possibility for captured insects to find their way out again.

The trap only gives a sample of specimens flying near the water-surface and from one point in the cross-section of the channel. Field observations on *Ephemera danica* and other characteristic species do not indicate this to be any essential source of error.

When a lot of insects accumulate in the upper compartment of the trap, this part may function as a »perfume centre». The captives constantly irritate each other, but also courtship and copula are frequent. Thus repellents as well as attractants, e.g. sexual perfumes, are diffused, and may, in addition to fumes of the anaesthetic, be active on the lee side of the trap. However, the »perfume centre» comes to stand about 1.5 m above the upper edge of the entrance, and no clustering around it has been observed, nor does the material bear witness of such a source of error.

Of much greater influence upon the results seems to be relatively strong wind parallel to the long axis of the trap. Its effect is exactly opposite for the two halves of the trap — accumulating to the windward, depleting to

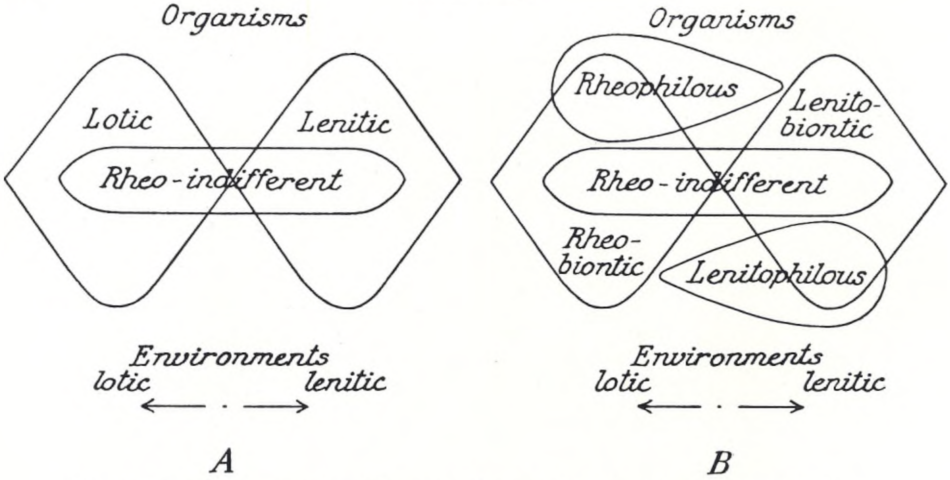

Fig. 4. Ecological grouping. The models are not designed to be quantitative.

the leeward — but only the lower compartment is more profoundly affected. Traces of this effect are discernible, and will be discussed more closely below.

Material. The catches were preserved in 80 % alcohol. *Trichoptera* (except for the genus *Hydroptila*) and *Plecoptera* have been determined to species, *Ephemeroptera* to genus, while the rest has been classified to family. The nomenclature follows FORSSLUND & TJEDER (*Trichopt.*), BRINCK (*Plecopt.*), and TULLGREN—WAHLGREN (remaining insects).

Definitions. On the basis of informations in literature about the preimaginal development phases, supplemented with reference to *Trichoptera* from the author's unpublished investigations in the River Ammerån district, the material has been placed into three provisional ecological groups as follows, cf. Fig. 4 A. This grouping concerns the investigated area, and makes no pretence to universal validity. Lotic is used here according to NEEDHAM and LLOYD (1916, p. 315) in the sense of mobile water with no demand for a uniform direction of current. Thus the genuine surf-zone insects of lakes are included in this group.

1. *Lotic insects.* Exclusively in lotic environments, in standing water only as vicini or alieni.
2. *Rheo-indifferent insects.* Both in moderately lotic and lenitic environments without showing preference for one or the other.
3. *Lenitic insects.* Exclusively in lenitic environments, in mobile water only as vicini or alieni.

It would have been desirable to classify the material ecologically into five groups, according to Fig. 4 B, and thus applying to the term lotic its modern import of water moving in one direction, but the autecology of the different species is too inadequately known to permit such a fine-grade classification.

Table 1. The flight directions of *Trichoptera* in relation to the direction of the water-current as shown by net-catching. Number of individuals of each sex flying up- or downstream (U and D, resp.)

Species etc.	Sample 1				Sample 2				Samples 1 + 2			
	♂♂		♀♀		♂♂		♀♀		♂♂		♀♀	
	U	D	U	D	U	D	U	D	U	D	U	D
Lotic insects												
Rhyacophila nubila Zett.	—	—	1	—	1	—	—	—	1	—	1	—
Agapetus comatus Pict.	—	—	—	—	—	—	5	1	—	—	5	1
Ithytrichia lamellaris Eat.	—	—	—	—	4	1	2	2	4	1	2	2
Hydroptila sp.	—	—	—	—	—	—	—	1	—	—	—	1
Neureclipsis bimaculata L.	—	—	—	—	2	3	1	—	2	3	1	—
Psychomyia pusilla F.	—	—	—	—	—	—	1	—	—	—	1	—
Hydropsyche pellucidula Curt.	2	—	25	7	—	—	1	—	2	—	26	7
» *instabilis* Curt.	2	3	56	21	33	22	17	7	35	25	73	28
Cheumatopsyche lepida Pict.	2	2	—	—	2	1	26	10	4	3	26	10
Lepidostoma hirtum F.	—	—	—	—	1	—	15	3	1	—	15	3
Lotic insects, total	6	5	82	28	43	27	68	24	49	32	150	52
Lenitic insects												
Limnophilus fuscicornis Ramb.	—	—	—	—	—	—	1	—	—	—	1	—

IV. The experiments

1. *Preparatory experiments, net-catching*

Methods, see p. 171.

Experimental conditions. Sample 1. 2-VII-1953, 23.30—00.10 o'clock. Air-temperature +14°.0—+13°.5 C, rh 80—82 %, wind NNW 1 Beaufort, i.e. downstream and parallel to the river course. Surface velocity of the water current in the middle of the channel 1.8 m/sec., at the sampling place 0.5 m/sec.

Sample 2. 10-VII-1953, 21.30—22.00 o'clock. Air-temperature +13°.5—+12°.5 C, rh 88—90 %, wind a feeble draught downstream. Surface velocity of the current as above.

Results and discussion. Of the catches only *Trichoptera* were taken care of. Sample 1 contained 121, sample 2 163 specimens. The material was almost exclusively made up of lotic species, and is accounted for in Table 1. As sampling conditions were almost equivalent the material has been treated *en bloc.*

Of 283 lotic insect specimens 199 (70 %) flew upstream, while 84 (30 %) flew downstream. 202 specimens were females, of which 150 (74 %) flew upstream, while 52 (26 %) flew downstream. Only 1 lenitic form was caught.

The methods of this experiment are impaired by too many sources of error to permit a detailed treatment of the material. However, a predominantly upstream direction of flight in the females of these lotic species is indicated both in isolated species and in the material *en bloc*. For the purpose of further discussion it is worth noting that the wind was blowing downstream.

2. *Main experiments, insect trapping*

Methods, see p. 171 ff.

Experimental conditions. Sample 3. 5-VIII-1955 20.00 o'clock—7-VIII-1955 8.00 o'clock, 36 hours.

Sample 4. 3-IX-1955 17.00 o'clock—6-IX-1955 10.00 o'clock, 41 hours. The latter had to be taken during a somewhat longer time, insects being scarce in the autumn. Weather-conditions and approximate flight-activity of some chosen insects have been compiled in a *bioclimatogram* for each sample, Fig. 5. The wind, when noticeable, was gusty, and the plotted velocities represent round maxima. The velocity of the surface water-current was 1.7—1.7 m/sec. in the middle of the channel, and 0.5—0.4 m/sec. under the trap, respectively.

The Material

Of the rich catches only aquatic insects have been treated so far, of sample 3 4046 specimens, of sample 4 1471 specimens. This material is accounted for in Table 2, p. 180 f.

In order to eliminate certain sources of error the following material has been excluded from the ecological group, to which it belongs. Nor have any conclusions been based upon it.

1. *Leptoceridae*. In *Leptoceridae* the males hover in swarms of up to several hundreds of specimens, zig-zaging to and fro some half metre above the surface of the water in very limited places along the banks. A gust of wind can move the entire swarm. Such a swarm, which happens to hit one entrance of the trap, can completely dislocate the results. The above behaviour is especially pronounced in the lotic species, e.g. *Athripsodes commutatus*.

2. *Chironomidae*. It has not been possible to classify all the material of *Chironomidae,* primarily not the females. Their autecology is furthermore too inadequately known to permit their complete division into ecological groups. For this reason they have been excluded from the analyses. However, it is worth while taking a glance at the figures.

As regards *Ithytrichia, Hydroptila,* and *Simuliidae* the objection can be raised that their minute sizes might permit them to make their way through the partition-wall between the two halves of the trap (meshes of the bobbinet 1.5 mm in diameter), a possibility further strengthened in the case of *Simuliidae* by their habits of creeping through the body-wear of their victims. However, only the specimens penetrating through the partition-wall in the lowest compartment of the trap will dislocate the results, and, as has been observed, only to a negligible degree. The effect will primarily be a levelling

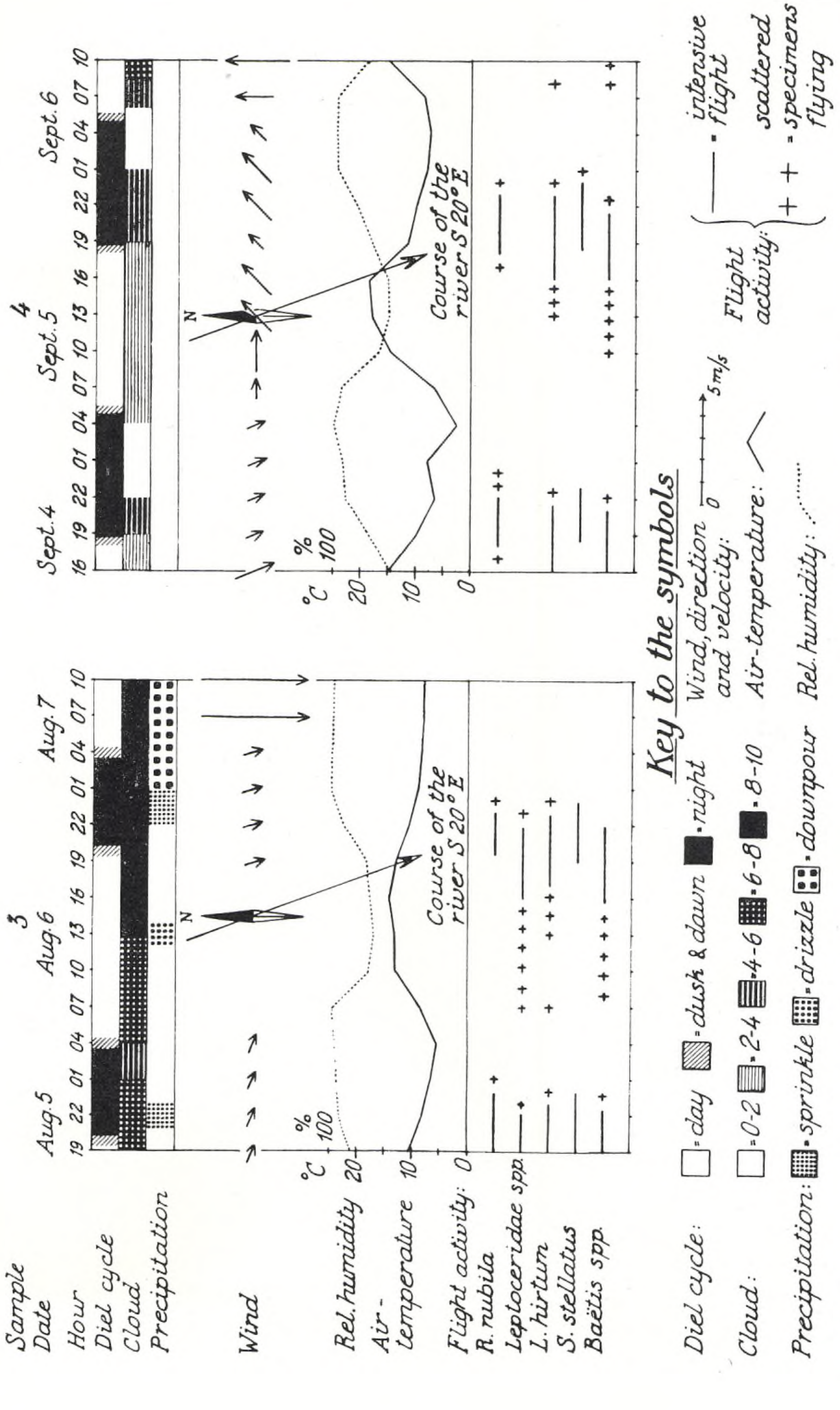

Fig. 5. Bioclimatograms showing weather conditions and approximate flight activity of some of the insects concerned during the trap experiments, furthermore direction of the course of the river.

between the catches in the two halves of the trap. Specimens creeping through the bobbinet in other parts of the trap will escape. This effect must be of the same relative importance for either half.

Weather conditions at the two dates of sampling show some similarities. Thus temperature and relative humidity do not differ fundamentally. During the later part of the night of Sept. 5th the temperature was too low for permitting any vigorous flight activity. Also the direction and velocity of wind were similar, viz. downstream and parallel to the river course, except during the later part of sample 4, when the wind gradually shifted to obliquely upstream, and increased in force. The effect of the direction of the wind will be further discussed below. Cloudiness and amount of precipitation show greater divergence. Sample 3 was taken in cloudy weather with increasing rain. This stimulated the noctiphilous water insects which could be seen on wing sporadically even at noon. During sample 4 the sky was clearer, and no precipitation fell. The diurnal flight periods of the sampled insects were more concentrated to dusk and night.

Thus, the two catches are treated separately, but on account of the great similarities in weather conditions an amalgamation is also made.

Results and discussion

1. Flight directions of lotic insects

Rhyacophila nubila may be chosen as a type of decided torrenticoles. Its larva is a free living predator in rapids with stony bottoms. It usually succumbs within a few hours in standing water. The figures indicate that the males fly about as much upstream as downstream. The downstream flight is somewhat preponderant in sample 4. This may be due to the shifting of the wind direction during the last few hours of the sampling. The flight direction of the females is predominantly upstream in either case, to a lesser degree in sample 4.

Cheumatopsyche lepida is another torrenticole. Its larva is a net spinning filtrator. The imago is a rather weak flyer which can not press against even moderate wind. The figures indicate a difference between the sexes in dominating flight direction. This is analogous to that of *R. nubila,* but not as distinctly pronounced. Moreover, cf. p. 184 f.

Neureclipsis bimaculata is a moderately lotic trichopteran, the larvae of which spin their nets on bottom objects and weeds in sections of the streams, where the current is regular, and where its velocity will rarely exceed 1 m/sec. I have also found them in Lake Solbergsvattnet on sunk timber in narrow channels, where current is present but not noticeable. There is some predominance for an upstream direction of flight in the males, but not at all of the same magnitude as in the females.

Baëtis and *Simuliidae,* too, contain exclusively lotic species. Unfortunately,

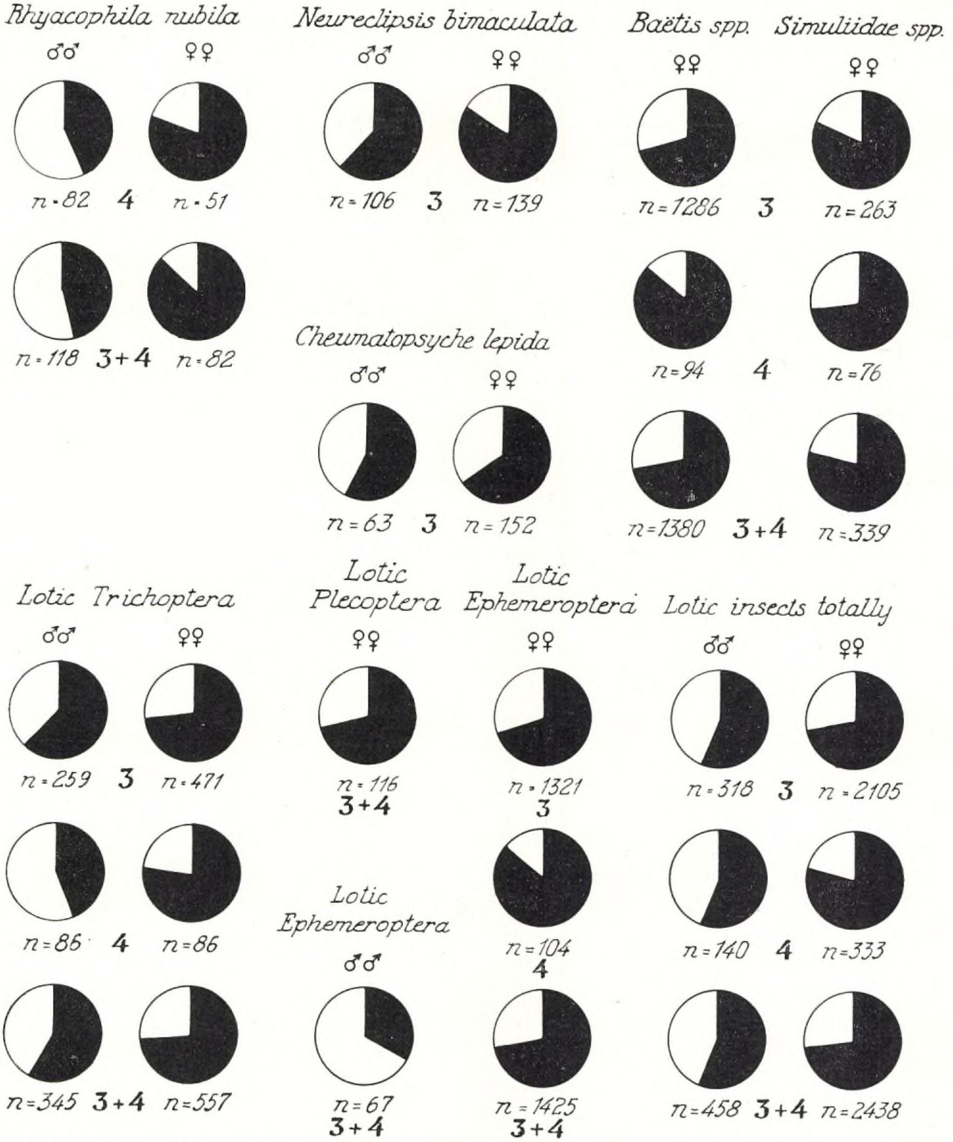

Fig. 6. The flight directions of lotic insects in relation to the direction of the water current. Percentage flying upstream (black sector) and downstream (white sector).

the males were very scarce in the material. The females, however, were multitudinous, and their flight decidedly upstream (70—80 %).

The other lotic species represented indicate the same distribution amongst up- and downstream flight, e.g. *P. pusilla, H. pellucidula, H. instabilis, L. hirtum, L. fusca,* and *I. grammatica,* but the material is scanty. Discrepancies in *Ephemeroptera* are caused by the presence of sub-imagines, a matter which will be discussed below, cf. p. 182 f.

Table 2. The flight directions of some aquatic insects in relation to the direction of the water current as shown by insect trapping. Numbers of individuals and percentages of each sex flying up- or downstream (U and D, respectively).

Species etc.	Sample 3								Sample 4								Samples 3 + 4							
	♂♂				♀♀				♂♂				♀♀				♂♂				♀♀			
	U		D		U		D		U		D		U		D		U		D		U		D	
	No	%	No	%	No	%	No	%	No	%	No	%	No	%	No	%	No	%	No	%	No	%	No	%
Lotic insects																								
Trichoptera																								
Rhyacophila nubila ZETT.	19		17		30		1		35	43	47	57	41	80	10	20	54	46	64	54	71	87	11	13
Agapetus comatus PICT.	—		—		1		—		—		—		—		—		—		—		1		—	
Ithytrichia lamellaris EAT.	22		2		28		27		—		—		3		4		22		2		31		31	
Hydroptila sp.	—		—		5		1		—		—		2		—		—		—		7		1	
Wormaldia subnigra MC LACHL.	—		—		—		—		—		—		3		—		—		—		3		—	
Neureclipsis bimaculata L.	66	62	40	38	117	84	22	16	1		—		1		—		67	63	40	37	118	84	22	16
Polycentropus flavomaculatus PICT.	4		—		1		1		—		—		1		—		4		—		2		1	
Psychomyia pusilla F.	6		2		14		4		—		—		—		—		6		2		14		4	
Hydropsyche pellucidula CURT.	1		1		10		5		—		—		—		—		1		1		10		5	
» *instabilis* CURT.	3		2		19		6		—		—		—		1		3		2		19		7	
Cheumatopsyche lepida PICT.	36	57	27	43	98	65	54	35	1		1		9		1		37	60	28	40	107	66	55	34
Molannodes tincta ZETT.	1		—		—		—		—		—		—		—		1		—		—		—	
Lepidostoma hirtum F.	4		4		22		5		—		—		4		3		4		4		26		8	
Anabolia nervosa LEACH.	—		—		—		—		—		—		1		—		—		—		1		—	
Stenophylax stellatus CURT.	—		2		—		—		1		—		1		1		1		2		1		1	
Trichoptera, total	162	62	97	38	345	73	126	27	38	44	48	56	66	77	20	23	200	58	145	42	411	74	146	26
Plecoptera																								
Nemoura borealis MORT.	—		—		—		—		—		—		15		11		—		—		15		11	
Leuctra digitata KEMPN.	—		—		—		—		—		—		1		1		—		—		1		1	
» *fusca* L.	—		—		—		—		13		6		34		3		13		6		34		3	
Isoperla grammatica PODA	—		—		32		17		—		—		—		1		—		—		32		18	
Chloroperla burmeisteri PICT.	—		—		—		1		—		—		—		—		—		—		—		1	
Plecoptera, total	—		—		32		18		13		6		50		16		13		6		82	71	34	29
Ephemeroptera																								
Heptagenia spp.	1		16		—		3		—		—		—		—		1		16		—		3	
Ecdyonurus spp.	6		3		11		7		1		—		—		—		7		3		11		7	
Paraleptophlebia spp.	—		10		—		—		—		—		—		—		—		10		—		—	
Ephemerella spp.	1		6		2		12		9		3		9		1		10		9		11		13	
Baëtis spp.	4		6		915	71	371	29	—		1		82	87	12	13	4		7		997	72	383	28
Ephemeroptera, total	12		41		928	70	393	30	10		4		91	86	13	14	22	33	45	67	1019	72	406	28
Coleoptera																								
Helmis aeneus MÜLL.	—		—		—		—		—		—		1		—		—		—		1		—	

Diptera																								
Simuliidae spp.	3		3		212	81	51	19	17		4		56	74	20	26	20		7		268	79	71	21
Lotic insects, total	177	56	141	44	1517	72	588	28	78	56	62	44	264	79	69	21	255	56	203	44	1781	73	657	27
Rheo-indifferent insects																								
Trichoptera																								
Limnophilus rhombicus L.	—		—		1		2		—		—		—		—		—		—		1		2	
» *borealis* ZETT.	—		—		—		—		1		1		1		—		1		1		1		—	
» *flavicornis* F.	—		—		1		—		—		—		—		—		—		—		1		—	
Plecoptera																								
Nemoura cinerea RETZ.	—		—		—		—		—		—		1		—		—		—		1		—	
Ephemeroptera																								
Leptophlebia sp.	1		—		2		12		—		—		—		—		1		—		2		12	
Caenis sp.	—		1		—		—		2		—		1		—		2		1		1		—	
Centroptilum spp.	—		—		—		—		10		29		14		17		10		29		14		17	
Rheo-indifferent insects, total	1		1		4		14		13		30		17		17		14		31		21		31	
Lenitic insects																								
Trichoptera																								
Cyrnus trimaculatus CURT.	—		—		—		—		—		1		—		—		—		1		—		—	
Phryganea grandis L.	—		—		—		1		—		—		—		—		—		—		—		1	
Nemotaulius punctatolineatus RETZ.	—		—		—		1		—		—		—		—		—		—		—		1	
Limnophilus elegans CURT.	—		—		1		—		—		—		—		—		—		—		1		—	
Ephemeroptera																								
Cloëon sp.	—		—		—		—		1		6		8		4		1		6		8		4	
Lenitic insects, total	—		—		1		2		1		7		8		4		1		7		9		6	
Excluded material																								
Trichoptera																								
Athripsodes alboguttatus HAG.	4		4		2		1		—		1		—		2		4		5		2		3	
» *annulicornis* STEPH.	1		—		—		—		—		—		—		—		1		—		—		—	
» *cinereus* CURT.	3		—		—		—		—		—		—		—		3		—		—		—	
» *albifrons* L.	1		—		—		—		—		—		—		—		1		—		—		—	
» *commutatus* MCLACHL.	196		34		16		6		2		1		—		—		198		35		16		6	
» *dissimilis* STEPH.	—		—		3		3		—		—		—		3		—		—		3		6	
Mystacides azurea L.	—		1		—		—		—		—		—		—		—		1		—		—	
Trichoptera, total	205		39		21		10		2		2		—		5		207		41		21		15	
Diptera																								
Chironomidae spp.	71	53	64	47	837	70	353	30	108	63	63	37	525	73	196	27	179	58	127	42	1362	71	549	29

The material treated *en bloc* gives the same picture of the flight directions of the sexes as the chosen types. This is valid for isolated orders and samples as well as for the whole material. Moreover, cf. Fig. 6 and 7.

2. Flight directions of rheo-indifferent insects

No species is sufficiently numerous in the catches to be treated separately. Nor does the whole material permit more than the statement that there is no evidence for a predominance of upstream flight either in males or in females.

3. Flight directions of lenitic insects

The material of lenitic insects is too scanty to be treated at all.

4. Excluded material

It can be of some interest to scrutinize the figures for *Chironomidae.* The distribution amongst up- and downstream flight for both sexes is analogous to that of the lotic species above. The material of the females shows a convincing predominance for upstream flight, 70, 73, and 71 %, as compared with downstream flight, 30, 27, and 29 %. The males tend more to an even distribution, 53, 63, and 58 % upstream, and 47, 37, and 42 % downstream. As the material was taken in a pronounced section of rapids, 2 km from the outflow, its bulk must be supposed to be made up of lotic species.

Summing up, the experiment reveals that 70—80 % of the females of lotic insects of different orders, when swarming over a rapid, keep the upstream direction. On the other hand the males do not manifest any distinctly predominant flight direction either up- or downstream. The material does not always contain adequate numbers of the separate species, but its width must be sufficient, and the tendency is uniform throughout. On this account it must be permissible to ascribe to the obtained results a general validity for lotic insects.

Before further discussing the results from a biological point of view a feature in the female material giving some valuable informations shall be dealt with.

The effect of egg maturity upon the flight behaviour of the females

The material of lotic ephemeropterans was made up of imagines and to a lesser degree of sub-imagines, cf. Table 3. In the male sex the sub-imagines do not diverge from the imagines with regard to flight direction. The predominance of downstream flight, suggested by the scanty material, may be due to the downstream wind as these insects are no strong flyers. In the females, however, the flight of the sub-imagines is predominantly downstream, just the reverse of conditions in the imagines. This may be due to the inferior power to fly of the newly emerged sub-imagines, the flight direction of which is governed mainly by the wind. Since the sub-imagines of the genera in question are not capable of mating, another though remote possibility will

Table 3. Flight direction in relation to the direction of the water current in lotic ephemeropterans as shown by insect trapping, sample 3. Numbers of imagines and sub-imagines of each sex flying up- or downstream.

Genus	♂♂				♀♀			
	Upstream		Downstream		Upstream		Downstream	
	Im.	Subim.	Im.	Subim.	Im.	Subim.	Im.	Subim.
Heptagenia	1	—	5	11	—	—	1	2
Ecdyonurus	1	5	—	3	5	6	1	6
Paraleptophlebia ..	—	—	9	1	—	—	—	—
Ephemerella	1	—	3	3	1	1	2	10
Baëtis	4	—	1	5	912	3	348	23
Total	7	5	18	23	918	10	352	41

open, to the effect that the instinct of upstream flight may not develop until after impregnation or even after fertilization of the eggs, i.e. in any way in connection with the maturation of the eggs. It is worth while to examine these matters.

The nucleus of the insect egg does not undergo maturation divisions until the spermatozoon has entered the plasm (DEMEREC 1950, and others). According to ruling conceptions the fertilization takes place after the ovulation, i.e. when the egg is furnished with yolk and chorion. The egg, when passing the opening of the receptacular duct in the vagina, receives one or more spermatozoa which enter through the micropyle.

In some insects (*Cimex,* viviparous *Chrysomelids,* the polyctenid *Hesperoctenes, Capsids*), however, the fertilization takes place while the egg is still very small, and lies in the ovary. Thus in some *Capsids* the spermatozoa enter the ovarioles, and penetrate the oöcytes in the vitellarium before the chorion is formed (KULLENBERG 1944, p. 431 ff.). In *Cimex* fertilization is not possible after that chorion has been formed (ABRAHAM 1934).

As far as I know these conditions have not been studied in *Trichoptera.* It might, however, be suspected that the impregnation will in some way affect the oögenesis or the oviposition also in these insects. This is normal within the class of insects (cf. WIGGLESWORTH 1950). Thus in certain cases impregnation has been found to release the development of the oöcytes, or to have an accelerating effect upon the egg production. In other cases it has a stimulating or releasing effect upon the oviposition. Concerning these problems I have made the following observations on trichopterans.

A female caught in the wild of *Halesus radiatus* CURT. was caged, and kept on sugar solution. In her captivity she was accompanied by two males. Immediately after the capture, on Aug. 27th, she laid a batch of eggs, and then copulated. A fortnight later, on Sept. 11th, she laid a new egg mass, and then again copulated. The last oviposition occurred after a further 17 days, on Sept. 28th, but then the female died. The number of eggs in the batches decreased for each oviposition (119, 78, and 46). In the periods between the ovipositions her activity was very low, and she was not disposed to mate in spite of the passionate courtship display of the males. The experiment was carried out at a rather low temperature (+5—+10°C). Caged *Limnophilus femoratus* ZETT. have revealed an analogous periodicity in copulation and oviposition. It seems plausible that the intervals are taken up by the maturation of an egg portion after impregnation. However, matters have so far not been examined microscopically. In any case the females with immature eggs do not show the same flight behaviour as those ready for oviposition. This will be clear from the following examination.

A random sample of the material of females of two decided lotic trichopterans, *C. lepida* and *R. nubila,* were dissected in order to decide whether their eggs were mature or not. Already the exterior of the specimens preserved in alcohol gave informations in the question. Females with ripe eggs had a distended, firm abdomen with the large eggs visible through the wall. The abdomina of immature females, on the other hand, were flabby and not distended, and the unconsumed fat body rendered the body wall opaque. The abdomina were opened, and the development of the eggs was classified as mature or immature. The presence of a chorion was taken as a criterion of maturity. Immature eggs were subdivided in "undeveloped" and intermediate. In every individual specimen of the two species a great number of eggs turned out to stand upon about the same phase of development, either mature, intermediate, or "undeveloped". In *C. lepida* the long axis of the ripe eggs was about 0.31 mm, that of the "undeveloped" 0.07 mm. In *R. nubila* these figures were 0.30 and 0.04 mm. The figures refer to alcohol preserved and hence shrunk eggs. In only 23 cases of 203 specimens females with oöcytes of intermediate sizes were met with. In every separate case also these oöcytes appeared to be of about the same size, forming a batch. In some females the abdomen was almost completely filled with ripe eggs, in others only partly. This may be due to the circumstance, whether the female is going to lay eggs for the first time or for the second or third, the number of eggs in the laid batch decreasing with each oviposition (cf. above, *H. radiatus*). The scanty presence of females with eggs of intermediate development indicates that the flight activity during maturation may be rather low.

The observations on the caged *H. radiatus* and *L. femoratus* as well as this examined trap material suggest that the oögenesis takes place simultaneously for a limited portion of oöcytes forming a batch of eggs. It seems probable that impregnation stimulates or even releases the oögenesis. After an interval closed by oviposition a new portion of oöcytes starts developing, probably not until the female has mated again.

The distribution of females with mature or immature eggs amongst up- and downstream flight is shown in Fig. 7. The predominance of upstream

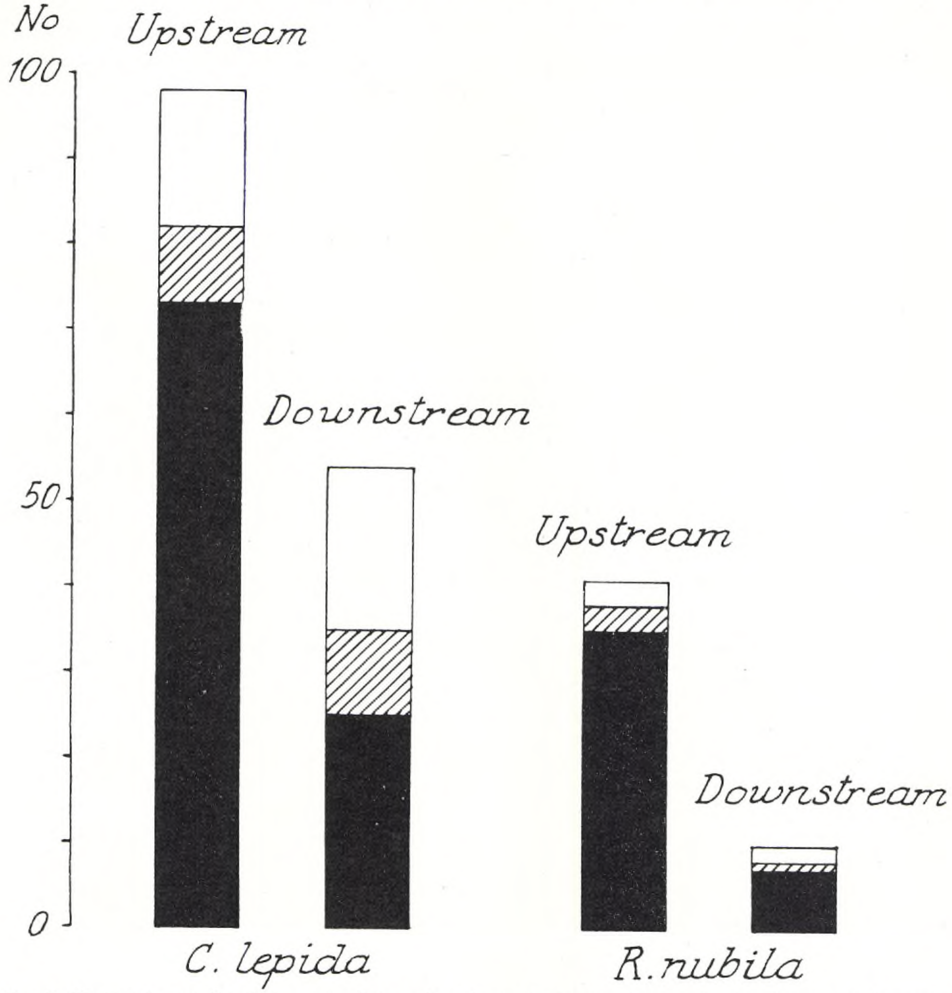

Fig. 7. State of egg development of two female lotic trichopterans in specimens flying upstream and downstream. Mature eggs (black), intermediate (hatched) and "undeveloped" eggs (white).

flight in females ready for oviposition is quite distinct and significant. The females with immature eggs, on the other hand, do not show any preference for one or the other direction of flight. The sample of *C. lepida* must be adequate, and that of *R. nubila* indicates the same tendency. It may thus be stated that the instinct of upstream movement develops during the oögenesis, and is distinct when the female starts for oviposition. Until the oögenesis has set in such an instinct is not discernible.

According to the above the predominance of upstream flight may be more pronounced than is indicated in Table 2 and Fig. 6, as the figures may include a number of immature females.

V. A general discussion of the flight of the insects concerned

1. *The flight of males and of females with immature eggs*

In many cases insects disposed for copulation exhibit a kind of dancing flight, connected with their gathering in larger or smaller swarms. The size of the swarm and the pattern of flight can be specific for certain species or groups of species. Instances of this are given in most insect orders. Such swarms will often be made up exclusively of males. Now and then one or several males detach themselves from the swarm, and attack passing females or even insects outside the own species. This type of flight is outside the scope of the adopted methods, as the catching area of the insect trap, 5.4 m^2, is too small a part of the cross-section of the flight space to give valid samples of clustering insects.

However, there are many insects which do not fly in marked clusters. They search after the other sex in a flight which represents an ever repeated trial and error in all directions until proper external stimuli direct the flight. Then the males will often be more active in their search than the females. Also clustering insects exhibit this type of flight outside the swarm. The results of the trapping experiments, concerning the flight of the males and the immature females, are quite in accordance with these states of matters. A greater representation of males could possibly have been expected, their flight activity within or near their normal habitat being generally higher than that of the females. The under-representation largely affects clustering types, such as ephemeropterans.

The poor representation in the material of females, the oögenesis of which stands at an intermediate stage, may be interpreted as sign of a period of relatively low flight activity intercalated between copulation and oviposition.

2. *The flight of females with mature eggs*

Though the flight activity of female insects generally is rather feeble as compared with that of the males, they are known to carry out extensive displacements. The trap experiments have shown a predominance of upstream flight in the females concerned. It would be of great interest to know how far they extend this upstream flight, but no decision is possible so far. Still the following observations indicate that they may cover long distances.

1. During the last few years I have accidently captured the following species of lotic *Trichoptera,* attracted by ordinary electric bulbs at my home: *Plectrocnemia conspersa* CURT., *Arctoecia concentrica* ZETT., and *Stenophylax stellatus* CURT. The locality lies 2—5 km from the nearest streams, where their larvae are to be found. All finds were females.

2. On Sept. 20th 1956 a net sample was taken in Lake Solbergsvattnet 1 km from the outflow through River Ammerån. A feeble wind was blowing

from a westerly direction, i.e. in direction towards the outflow. The following lotic insects were caught: *R. nubila* 2 ♀♀, *Apatania stigmatella* ZETT. 2 ♀♀, and *Simuliidae* 1 ♂, 2 ♀♀. They all kept the direction against the wind, thus upstream.

3. On July 9th 1956 I caught by net some insects at different places in Lake Solbergsvattnet. Also this time the wind was blowing from NW. The first capture was made 2 km from the outflow, and contained the following lotic species: *Nemoura borealis* 1 ♂, 2 ♀♀, *R. nubila* 1 ♀, *A. comatus* 1 ♀, *N. bimaculata* 4 ♂♂, 5 ♀♀, *H. instabilis* 2 ♀♀, *C. lepida* 1 ♀, and *L. hirtum* 20 ♀♀ (8 carrying egg batches!). The frequency of these species was much greater than this little sample proves. Particularly *L. hirtum,* in its characteristic fluttering flight, was numerous. From among the mentioned species *N. bimaculata* is the only the larvae of which have so far been found in the lake, and, what is more, only in certain channels. The caught specimens all flew against the wind. Another kilometre up the lake *N. bimaculata, H. instabilis, C. lepida,* and *L. hirtum* still were captured steadily flying against the wind, and at Lake Fyrsjön, 5 km in direction upstream from the rapids of Ammerån, scattered females of *H. instabilis* and *L. hirtum* were met with.

These observations indicate that the females of lotic trichopterans actively move upstream for long distances. They probably cross small lakes along the river courses, and enter new stream sections. This may be valid also for other lotic insects. There is, however, a marked decrease in the number of upstream flying females as soon as the uppermost rapid of a river section is passed, and unruffled water is reached. This in combination with the periodically high density of larvae in the outlets, demonstrated by several scientists, (e.g. MÜLLER 1954 a, 1954 b, ILLIES 1956), indicates that the majority of the females for some unknown reason stop there, and deposit their eggs.

3. *Factors guiding the orientation of insects in relation to the water current*

A question of great interest is how the flying females can find their bearings upstream. On this no facts are available, and the problem seems to be extremly complicated. Actually no type of the chief senses can with certainty be eliminated from the discussion. There seems to be a co-ordination of multiple stimuli. This is suggested by the following instance.

A little brook discharges into River Ammerån in the middle of a rapid. The summer temperature of the brook rarely exceeds 10°C, that of the river being about 18—20°C. The adult meso-warm-stenothermal insects of the river fauna do not seem to enter the brook in appreciable numbers. Thus, for instance, *N. bimaculata, P. flavomaculatus,* and *Hydropsyche* spp., which on a certain occasion were numerous along the banks of the river, were caught only in scattered specimens along the brook up to 50 m from its outlet, but disappeared then totally. On the other hand the cold-stenothermal

Stenophylax latipennis CURT. from the willows around the brook was absent from the river. The catches were carefully taken by means of a net, 80 cm in diameter.

Some special observations on wind conditions raised the question whether the wind in combination with sign stimuli might enable moving females to find their bearings upstream. They seem to be worth mentioning.

During the trap experiments the wind was principally blowing downstream. The same direction of wind characterized the evenings when moving lotic females were sampled in Lake Solbergsvattnet. The investigated locality is a marked valley, cf. Fig. 1, the topography of which partly governs the direction of the local winds, deflecting them to prevailing upstream or downstream along the valley. This is illustrated by the wind arrows in Fig. 1. The records were taken on Aug. 28th 1956 at a height of 2 metres above the substratum in the course of 5 hours, and started and ended on the Cambro-Silurian plateau to the south of Lake Fyrsjön, where the conditions concerned remained essentially unaltered during the same time. The different valleys deflected the current direction of the ground-near air strata so as to be almost parallel to the dells. The deviation could be as much as 135° — from WNW to ENE —, but the velocity of the wind was at the same time greatly reduced.

According to GEIGER (1950, p. 256, Fig. 126, after DEFANT) there exists in calm weather a diurnal pattern for the local winds in a valley. Briefly, the warming up through insolation in the daytime causes winds in the direction up the valley, while the cooling through irradiation at night gives rise to winds of the reverse direction. The reversal occurs after sunrise and sunset with a short intervening period of calm.

Moreover, the friction between the flowing water and the air stratum immediately above is sufficient to bring about micro-winds in downstream direction. This can be readily demonstrated in calm weather by means of smoke.

Accordingly there are in marked valleys some given conditions for a predominance of winds in direction either up or down the valley. When the weather in the surrounding country is calm, there develops a smooth wind down the valley during that part of the day during which the majority of here treated insects deploys their main flight activity, cf. Fig. 5. Such a valley topography would, indeed, be an ordinary characteristic of the pronounced lotic environments, i.e. rapids and falls. In these those organisms are to be found which have gone farthest in lotic adaptation, and here the stream drift can rise to an intensity which interferes with the continued existence of the population of species.

Also a stream of a plain can be imagined to be accompanied by analogous wind conditions. The velocity of the water current being high enough to permit the existence of a lotic fauna, the stream also has the power of erosion, and runs its course in a ravine, cut down in the plain. Trees and shrubs along the banks also produce a type of valley topography as far as the wind conditions are concerned. HARRIS (1952, p. 53) notices that adult ephemeropterans appear to be attracted to roads and foot-paths, especially when the surface is wet. He has even observed females to lay eggs on them. At the locality of my investigation a road passes along the valley at a distance of 300 metres from the river. It forms a furrow in the wood carpet. At least *Ephemera danica* and *Sericostoma personatum* usually fly in fairly great numbers along this road, and, to judge from mere observations, predominantly in the direction up the valley.

If the mere head-wind had a positive effect in directing or attracting the flying females, the result would be their orientation or flight upstream (cf. SCHWINCK 1954).

In the expectance of facts, however, the question of how lotic female insects can find their bearings upstream must be left open. It will be of great interest to study the flight directions at a moderate wind from downstream.

VI. The biological signification of the results

The upstream migration — the colonization cycle

The trap experiments have proved that there exists a mass movement of females in the upstream direction along the investigated river. This movement is confined to females with mature eggs, and is active as the insects press on against the wind. The flight can continue over long distances, but the majority of the females stops at the uppermost rapid, when quiet water is reached. Here a rich oviposition must take place, since an accumulation of progeny appears. The motive for the movement thus must be the oviposition. The phenomenon thereby fulfills a criterion of migration, and can be termed *upstream migration.*

The established upstream migration of lotic female insects carries clear evidence for the colonization cycle, proposed by MÜLLER (1954 a). In spite of the copious production of progeny in nature the depopulating effect of high waters and the thinning effect of normal water currents will hazard the continued existence even of well adapted lotic species in their habitats. The upstream migration of the females for oviposition is a simple solution of the problem of recolonization. The most disadvantageous effect attached to this solution — local accumulation of the progeny to such an extent that keen and progressive competition will develop — is counteracted by the effect of the water current, as this involves both copious food supply of drifting organisms for passive filtraters, permitting a very high population density, and a downstream distribution of the progeny. It seems to be appropriate that the instinct for upstream migration should be restricted to mature females. If this were not the case the local population of a species would be spread far beyond the limits of its habitat, resulting in diminished chances for the sexes to find each other for copulation.

VII. Summary

1. Preparatory experiments by net catching indicated a predominant upstream direction of flight in the females of lotic *Trichoptera*.

2. A Malaise's bilateral insect trap was used for the main experiments. It was modified by means of a vertical partition wall in such a way that the catches from the two opposite halves of the trap were kept apart, thus enabling to determine whether the insects had kept an upstream or downstream direction along the river.

3. By means of this trap a total of 5517 aquatic insect specimens were captured on two occasions of sampling. It was found that 70—80 % of the females of lotic *Trichoptera, Plecoptera, Ephemeroptera* and *Simuliidae* flew in the upstream direction, when there was blowing a feeble wind downstream. This behaviour was only to a lesser degree, if at all, to be found in the males. The material of rheo-indifferent and lenitic species gave no evidence as to a predominant flight direction in either sex. However, this material last-mentioned was inadequate.

4. Caged females of the trichopterans *Halesus radiatus* and *Limnophilus femoratus* revealed a periodicity of about a fortnight in copulation and oviposition. It is suggested that the impregnation releases or accelerates the development of the oöcytes, as is the case in several insects. The intervals found are suggested to be taken up by the maturation of an egg portion after impregnation.

5. In the trichopterans *Cheumatopsyche lepida* and *Rhyacophila nubila* it was found that females flying upstream predominantly carried mature eggs, while those which did not show any preference for one or the other direction of flight predominantly carried immature eggs. It is suggested that the instinct of upstream movement develops during the oögenesis and is distinct, when the female starts for oviposition.

6. Observations on *Trichoptera* indicated that lotic females could extend their upstream flight up to 5 kilometres from their habitat, crossing small lakes along the river course. The females were found to move actively against a feeble wind. The majority seemed to stop at the uppermost rapid of the river section, where oviposition probably took place.

7. There seems to be a co-ordination of multiple stimuli which guides the orientation of the females in relation to the water current. Among these there are some evidence of the wind being active. In a valley there are some given conditions for a predominance of local winds parallel to the course of the

valley. Thus the valley topography has a deflecting effect upon the winds, which has been gauged as much as 135°, moreover the diurnal valley-wind pattern involves up-valley winds in the daytime, and down-valley winds at night. Finally the friction between the flowing water and the air causes micro-winds in the downstream direction. The investigated insects are to a high degree crepuscular and nocturnal flyers, and were found to press on against the wind.

8. The proved mass movement of females in the upstream direction is active and confined to specimens ready for oviposition. Thus the phenomenon can be termed migration. It serves as a mechanism which ensures a balance and the retention of the population in its habitat. Combined with the stream drift it forms the colonization cycle, involving a downstream distribution of the progeny through the action of the water current, counteracted by an upstream migration of the females for oviposition.

9. The investigations were carried out on River Ammerån in the provins of Jämtland, Northern Sweden.

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VIII. References

ABRAHAM, R. 1934. Das Verhalten der Spermien in der weiblichen Bettwanze (*Cimex lectularius* L.) und der Verbleib der überschüssigen Spermamasse. *Z. Parasitenk. 6:559—591.*

BEAUCHAMP, R. S. 1932. Some Ecological Factors and their Influence on Competition between Stream and Lake-living Triclads. *J. An. Ecol. 1: 175—190.*

BORGH, T. 1927. The minutes of the "Zoologiska Seminariet" of 22-XII-1927 at the University of Uppsala. (Unpublished).

BRINCK, P. 1949. Studies on Swedish stoneflies. *Opusc. Entom. Suppl. XI: 1—250.*

CHANDLER, D. C. 1937. Fate of Typical Lake Plankton in Streams. *Ecol. Monogr. 7: 445—479.*

DEMEREC, M. 1950. *Biology of Drosophila.* New York. *1—632.*

DENDY, J. S. 1944. The Fate of Animals in Stream Drift when Carried into Lakes. *Ecol. Monogr. 14: 333—357.*

FORSSLUND, K.-H. & TJEDER, B. 1942. Catalogus Insectorum Sueciae. II. Trichoptera. *Opusc. Entom. 7: 92—107.*

FORSSLUND, K.-H. 1953. Additamenta ad Catalogus Insectorum Sueciae. II. Trichoptera. *Ibidem 18: 72—74.*

GEIGER, R. 1950. *Das Klima der bodennahen Luftschicht.* Braunschweig. *1—460.*

GEISLER, R. 1953. Eine selbständliche Brutfütterungsanlage auch in Schleswig-Holstein? *Der Fischwirt 3: 372—376.*

HARKER, J. E. 1953 a. An investigation of the distribution of the mayfly fauna of a Lancashire stream. *J. An. Ecol. 22: 1—13.*

— 1953 b. Account of the autumn meeting at Liverpool of The British Ecological Society. *Ibidem 22: 418.*

HARRIS, J. R. 1952. *An Anglers Entomology.* London. *1—268.*

IDE, F. P. 1942. Availability of aquatic insects as food of the speckled trout, *Salvelinus fontinalis. Trans. Seventh N. A. Wildlife Conference.* Washington, D.C. *442—450.*

ILLIES, J. 1956. Seeausfluss-Biozönosen lappländischer Waldbäche. *Ent. Tidskr. 77: 138—153.*

KNÖPP, H. 1952. Studien zur Statik und zur Dynamik der Biozönose eines Teichausflusses. *Arch. Hydrobiol. 46: 15—102.*

KRIEGSMANN, F. 1952. Zur Besatzbeschaffung für Still- und Fliessgewässer. *Allg. Fisch.ztg. 77: 453—455.*

KULLENBERG, B. 1944. Studien über die Biologie der Capsiden. *Zool. Bidr. Uppsala 23: 1—522.*

LEONARD, J. W. 1942. Some observations on the winter feeding habits of brook trout fingerlings in relation to natural food organisms present. *Trans. Am. Fish. Soc. 71: 219—227.*

MACAN, T. T. 1957. The Life Histories and Migrations of the Ephemeroptera in a Stony Stream. *Trans. Soc. Brit. Ent. 12: 130—156.*

MALAISE, R. 1937. A new insect-trap. *Ent. Tidskr. 58: 148—160.*

MOFFETT, J. W. 1936. A Quantitative Study of the Bottom Fauna in some Utah Streams variously Affected by Erosion. *Bull. Univ. Utah, Biol. Ser. 3: 1—33.*

MÜLLER, K. 1954 a. Investigations on the Organic Drift in North Swedish Streams. *Rept. Inst. Freshwater Research, Drottningholm 35: 133—148.*

— 1954 b. Faunistisch-ökologische Untersuchungen in Nordschwedischen Waldbächen. *Oikos 5: 77—93.*

— 1955. Produktionsbiologische Untersuchungen in Nordschwedischen Fliessgewässern. Teil 3. Die Bedeutung der Seen und Stillwasserzonen für die Produktion in Fliessgewässern. *Rept. Inst. Freshwater Research, Drottningholm 36: 148—162.*

— 1956. Das produktionsbiologische Zusammenspiel zwischen See und Fluss. *Ber. Limn. Flusst. Freudenthal VII: 1—8.*

NEEDHAM, J. G. and LLOYD, J. T. 1916. *The Life in Inland Waters.* Ithaca. N.Y.

NEEDHAM, P. R. 1928 a. A Quantitative Study of the Fish Food Supply in Selected Areas. *N. Y. St. Cons. Dept., Suppl. 17th Ann. Rept. 192—248.*

— 1928 b. A Net for the Capture of Stream Drift Organisms. *Ecology 9: 339—342.*

— 1929. Quantitative Studies of the Fish Food in Selected Areas. *N. Y. St. Cons. Dept., Suppl. 18th Ann. Rept. 220—232.*

— 1930. Ecology of Streams. *Biol. Lab., Long Island Biol. Assoc. 2: 3—6.*

ROEDER, K. D. 1953. *Insect physiology.* New York. *1—1100.*

SAWYER, F. E. 1950. Studies of the Sherry Spinner. *Salmon and Trout Mag. 129: 110—114.*

SCHWINK, I. 1954. Experimentelle Untersuchungen über Geruchssinn und Strömungswahrnehmung in der Orientierung bei Nachtschmetterlingen. *Z. vergl. Physiol. 37: 19—56.*

SCHÖNEMUND, E. 1930. Eintagsfliegen oder Ephemeroptera in Dahl's "*Die Tierwelt Deutschlands und der angrenzenden Meeresteile*". Jena.

STEINMANN, P. 1913. Über Rheotaxis bei Tieren des fliessenden Wassers. *Verh. naturf. Ges. Basel 24: 136—158.*

— 1915. *Praktikum der Süsswasserbiologie.* I. Die Organismen des fliessenden Wassers. Berlin.

Statens Meteorologisk-Hydrografiska Anstalt. 1944. Instruktioner Nr 505. Handbok för väderleksobservatörer. Stockholm. *1—113.*

Sveriges Meteorologiska och Hydrologiska Institut. 1946. Meddelanden Ser. E Nr 2. Internationell molnatlas. Stockholm. *1—36.*

THIENEMANN, A. 1925. *Die Binnengewässer. I.* Stuttgart. *1—255.*

— 1950. *Die Binnengewässer. XVIII.* Stuttgart. *1—809.*

TULLGREN, A. and WAHLGREN, E. 1920. *Svenska insekter.* Stockholm. *1—812.*

ULMER, G. 1927. Liste der deutschen Ephemeropteren und ihre Verbreitung. *Konowia 6: 234—262.*

WELCH, P. S. 1952. *Limnology.* New York. *1—538.*

WIGGLESWORTH, V. B. 1950. *The principles of insect physiology.* London. *1—544.*

WOLF, PH. 1947. Lax och Laxöring i Kävlingeån. *Skrifter från Svenska Lax och Laxöringföreningen 1: 79—84.*

WOLTERECK, R. 1908. Plankton und Seeausfluss. *Int. Rev. Hydrobiol. I: 303—304.*

ÅNGSTRÖM, A. 1946. *Sveriges klimat.* Stockholm. *1—105.*

Migration, Age, and Growth of the Brown Trout (*Salmo trutta* L.) in Lake Rensjön

By Sven Runnström

Content

Introduction

In 1940 the lake Rensjön was regulated by the erection of a dam at its outflow. The issuing river, Rensjöån, being considered an important spawning place for the population of the brown trout in Rensjön a ladder was inserted in the dam in order to allow the free passage of the fish between the lake and the river. In order to check the efficiency of the arrangement the fish ladder was constructed as a trap, daily observations of the ascent and descent of the trout in the ladder being carried out. During the year 1946 only the spawning run was observed, but since the beginning of 1947 daily observations were carried out during the entire season of migration. On the migrations during the years 1947 and 1948 the author has published a preliminary report (1949).

It was, however, desirable to extend the observations over a longer period in order to study the fluctuations in the migrations of the trout, in the growth of the fish, and in the strength of the year-classes. For this reason continuous observations have been carried out up to the year 1953, when it was intended to terminate the experiments. Since, however, the summer of 1953 exhibited certain special climatic features, which could be thought to influence the whole year-class formed in the course of this year, the checking was continued also during the years 1955 and 1956.

While in Norway the brown trout has been the object of examination in a great number of lakes, e.g. by DAHL (1910), HUITFELDT KAAS (1927), and SIVERTSEN (1952), only a limited literature exists on this fish in Swedish inland waters. ALM (1929) has examined the brown trout in one of our great lakes, viz. in Vättern, and ARVIDSSON (1935) has studied the migration of this trout by experiments with marking of fishes. GUSTAFSON (1951) has studied the movements and the age of trout in Lake Storsjön, and the author (1952), finally, has supplied some information about age and growth of the trout in some regulated lakes in the province of Jämtland. For this reason the author hopes that the studies presented below will contribute to an increased knowledge of the biology of the trout. The author is much obliged to Mr. EMIL ANDERSSON, Ånn, for his valuable assistance during the entire period of observations. Mr. Andersson has carried out all observations and experiments with marking at the fish ladder and the fences, and has during this time been compelled to live a very primitive life in this isolated place.

The Area of Investigation

Lake Rensjön is situated in the western part of Jämtland near the Norwegian frontier at an altitude of 500 ms. above sea-level, and belongs to the drainage system of the River Indalsälven. Rensjön forms the highest lake in the respective drainage system as can be seen from the map, Fig. 1, and is fed only by some smaller brooks. The lake is drained by the river Anjeälven which passes through some minor lakes, as Korsvattnet, Skärvattnet, and Summulsjön, before falling into the larger Lake Anjan.

Lake Rensjön covers a total surface of 47 sq.kms., and consists of two basins, viz. the larger Stor Rensjön and the smaller Lill Rensjön, which are connected by a sound. The greatest depth of Stor Rensjön is 134 metres, while Lill Rensjön, which only covers 2.97 sq.kms., is rather shallow.

The area of examination comprised in addition to Rensjön the river Anjeälven between Lill Rensjön and Lake Korsvattnet; this part of the river is known locally by the name Övre Rensjöån. The map, Fig. 2, show this part of the river to consist in its upper portion of four short rapids with strong current and of three intercalated pools with quiet water.

The lowermost rapid falls into Lill Korsvattnet which has the character of a smallish shallow lake. This in its turn discharges its water via a rapid into Lake Korsvattnet. The entire distance between Lill Rensjön and Korsvattnet measures about 1500 metres; of these the four upper rapids total 400 metres,

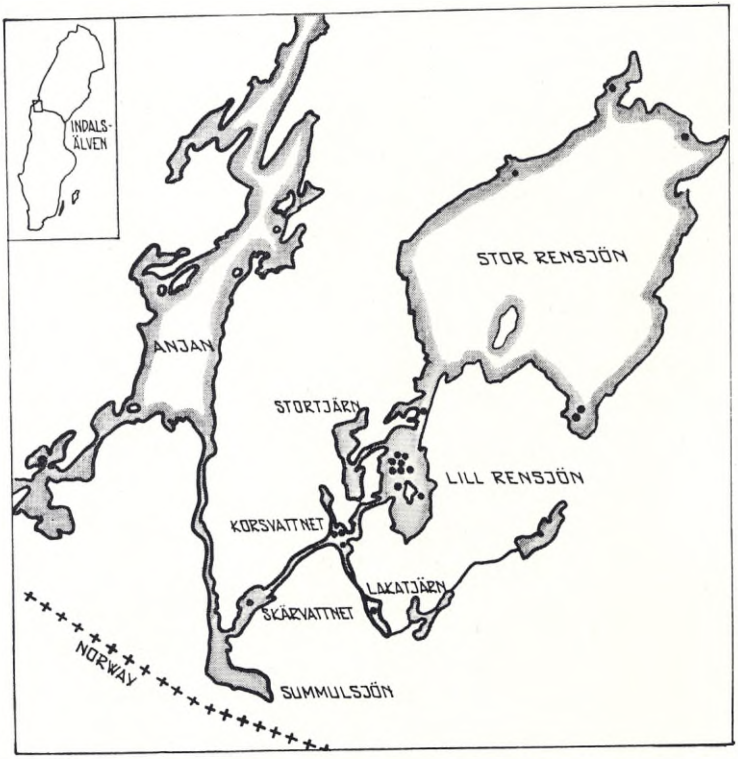

Fig. 1. The River Anjeälven and the Lakes Rensjön and Anjan.
Black dots indicate recaptures of spawning trout marked in the fish ladder.

while the rapid between Lill Korsvattnet and Korsvattnet is about 150 metres long. In the rapids the bottom is formed of gravel and stones, while the pools have bottoms of sediment.

The stock of fish in Lake Rensjön and in the lakes below it consists of char (*Salmo alpinus*), brown trout (*Salmo trutta*), and burbot (*Lota lota*). During later years grayling (*Thymallus thymallus*) has been introduced into Anjan, where it has augmented from year to year. A waterfall some hundred metres above the outlet of the Anjeälven into Anjan prevents, however, all movement of fish into the watercourse above it.

On account of the small number of the settled population and the distance of the lake from roads fishing in Rensjön is inconsiderable. The most important fishing takes place in autumn during the spawning of the char. A large form of char spawns in Lill Rensjön at the beginning of September, while the common alpine char spawns at the end of this month and at the beginning of November in the upper part of Stor Rensjön. When test fishing was carried out with fine-meshed nets also a dwarf char with developed gonads has been encountered in Lill Rensjön in the month of September. The yield

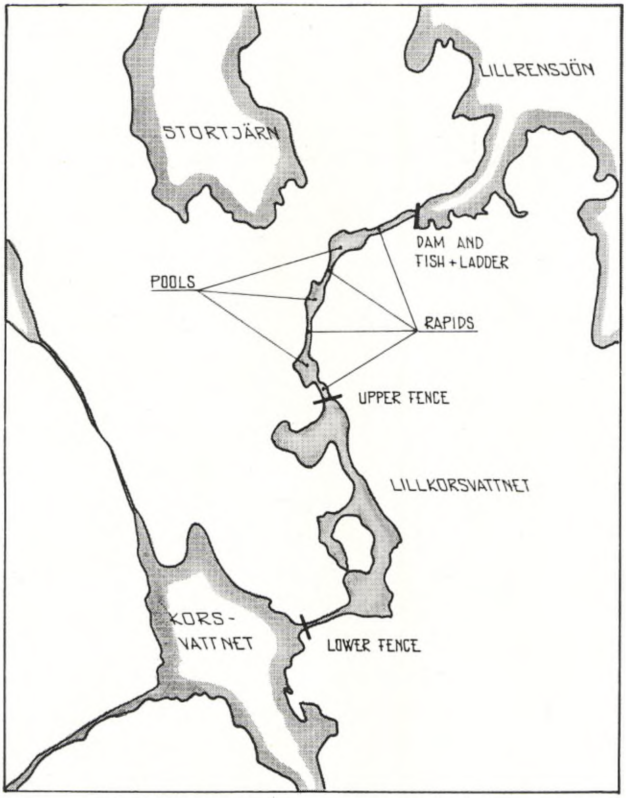

Fig. 2. The studied stream Övre Rensjöån.

of the entire lake amounts to about 1300 kg. or only about $^{1}/_{4}$ kg. per hectare (=2.471 acres). The greatest part of the catch consists of spawning char. The summer catch of brown trout is inconsiderable.

The fishing in Övre Rensjön is the property of a person who fishes there for sport. The river section is known for its fine large trout which descends into the river in August and September.

The Flow of Water in Övre Rensjöån

In the year 1940 Rensjön was regulated by the erection of a dam at the outlet of the lake, as mentioned already in the introduction (Cf. the map, Fig. 2). In this way a water reservoir was created for hydro-electric power plants farther downstream in the Indalsälven. During the summer the lake is dammed up 1.2 metres above normal highwater. In winter it is drained to 0.2 metres below normal low-water level. During the period of the damming-up the greater part of the water is stored in the lake in order to be let out

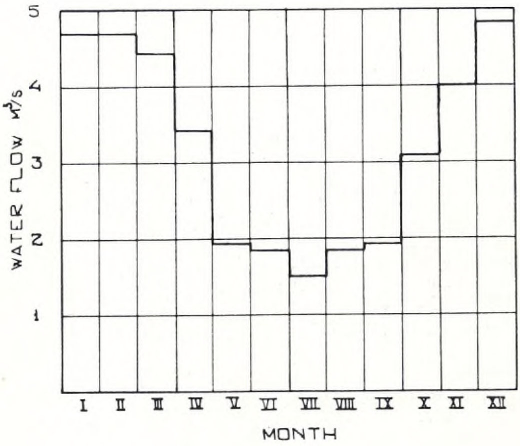

Fig. 3. The average seasonal fluctuations of the flow of water in the River Övre Rensjöån during the period 1943—1956.

during autumn and winter, when the power plants are most in need of water. Thus the regulated flow of the water in the river is the opposite of the natural one with the minimum flow in summer and the maximum in winter, as is evident from Fig. 3.

During the summer of 1941 and 1942 the dam gates were entirely closed, no water being allowed to run in the river during the months May to July. For the protection of the stock of trout it was decided later that a minimum amount of water of 1.6 m^3/sec. should be allowed to run down during August and September, and 1.0 m^3/sec. during the rest of the year. Of this amount 0.7—0.8 m^3/sec. is allowed to pass the fish trap, while the remainder is made to pass the dam gates. During the time of observation in the ladder the flow in the river has on the whole rather constantly amounted to between 1 and 2 m^3/sec., as appears from the diagram in Fig. 3.

Experimental Arrangements

In Fig. 4 the downstream view of the dam with the fish ladder is represented. The entrance and exit openings of the ladder have been provided with traps allowing the fish to enter the ladder from either direction, but preventing it from leaving. A frame with fine-meshed netting in the middle of the ladder separated fish coming from above and from below. Also the dam gate was covered with netting, leaving the ladder the only passage for the fish.

Usually the ladder was examined twice a day, when the numbers of fish migrating upstream and downstream were noted. After being measured and marked the fishes were again liberated either above or below the dam, depending on the direction in which their migration had taken place. The length of the fishes was measured as the distance from the tip of the nose to the tip of the terminal fin. For marking celluloid disks were used, and fixed with

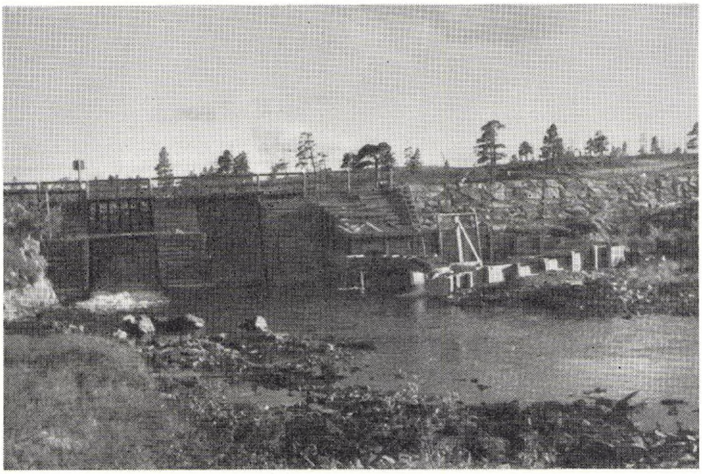

Fig. 4. Dam and fish ladder at the outlet of Lake Lill Rensjön.

nylon thread below the dorsal fin. On certain days distributed over the entire season of migration scales were collected of all fishes obtained in the ladder.

Since it was important not to kill the fishes the determination of the sex was possible only in the case of spawning fishes among which males and females could be distinguished by external characters. Only during 1955, when a number of fishes was killed for the examination of the stomach contents, the determination of sex and stage of maturity was carried out in a limited number of trout.

During the last four years of the observations the experimental arrangements were supplemented by a simple fence with traps for fishes migrating either downstream or upstream. This was set up at the outlet of Lill Korsvattnet into Korsvattnet, and is designated in the map, Fig. 2, as the lower fence. A similar fence was installed during 1955 and 1956 at the inflow to Lill Korsvattnet; this is designated in the map as the upper fence. Fig. 5 shows a photograph of the upper fence.

During the year 1955 fishing was carried out with an electrical shocker in the rapids between Lill Rensjön and Korsvattnet. Also test fishing with gill-nets of different mesh size took place both in the three pools of Övre Rensjöån and in Lill Korsvattnet. Also in Rensjön test fishing was carried out during several of the years of experimentation.

The Collected Material

Table 1 gives an account of the periods covered by the observations in the ladder, and of the number of fish which has passed the ladder during

Table 1. Fish captured in the fishladder and the fences in the period 1947—1956.

		Brown trout				Char	
Locality	Date	Spawning run		young fish run			
		up	down	up	down	up	down
Fishway	17/6—10/10 47	7	20	652	21	94	—
	20/4—16/10 48	9	34	1,024	27	124	13
	23/5— 7/10 49	24	11	582	2	79	1
	18/5— 3/10 50	6	15	596	2	103	1
	3/6—14/10 51	16	9	447	—	107	—
	6/6—30/9 52	9	4	480	—	76	1
	2/6— 8/10 53	21	16	503	—	68	2
	24/6—30/9 55	38	18	316	1	27	1
	19/6—30/9 56	8	4	352	1	21	—
	total	138	131	4,952	53	699	19
Upper fence	1/9—30/9 55	8	—	14	—	4	—
	25/6—21/9 56	3	1	88	25	14	4
	total	11	1	102	25	18	4
Lower fence	22/6—30/9 52	2	13	22	180	8	22
	16/6—28/9 53	7	—	75	230	27	17
	8/7—31/8 55	1	—	31	2	4	1
	2/7—28/9 56	13	—	33	26	42	11
	total	23	13	161	438	81	51

the course of every single year since the beginning of 1947. In most years the observations were started at the end of May or at the beginning of June, when the ice upon the lake had begun to melt, and were as a rule concluded at the beginning of October, when the first falls of snow used to arrive. In some years, however, the observations were begun either earlier or later, depending on the weather conditions.

Of the three species of fish occurring in the drainage system the trout is absolutely dominant in the fish ladder, but also a not inconsiderable number of char has taken part in the migration. In 1950 the ladder was checked also during the period from Jan. 30 to Febr. 15 in order to find out whether or not migration occcurred also during winter. During this time only 6 burbots were caught; this species of fish was absent in the ladder during the summer half-year.

On the basis of external inspection the trout has been divided into spawning fish and young fish. As far as the spawning fish is concerned the number of downstream migrating, mature trout (138) corresponds roughly to the number of ascending spent fish (131) for the entire series of observations. Nearly all young fish, or altogether almost 5000 trout, have been on their way up towards the lake, while an inconsiderable number (53) have been encountered on their descent. This remark applies also to the char in the fish ladder with altogether 699 ascending fishes as against only 19 descending.

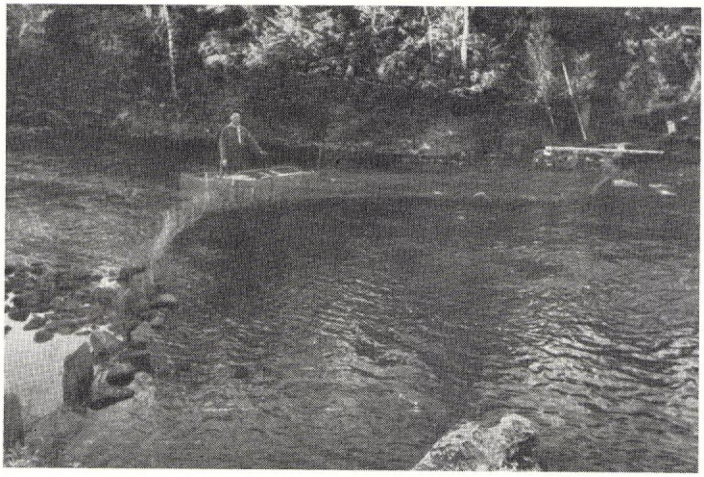

Fig. 5. Upper fence in the River Övre Rensjöån.

In the upper fence a certain ascent of spawning fish takes place from Lill Korsvattnet to Övre Rensjön, and also the young fish are preponderantly on the ascent. In the lower fence also an ascent of spawning fish takes place from Korsvattnet to the rapid above it, while the majority of the young fish descend towards Korsvattnet.

In Table 2 the results of the test fishing in Rensjön and in Övre Rensjöån in the summer of 1955 are shown. From a total length of the river of 169 metres with a breadth varying between 10 and 15 metres fishing with the el-shocker yielded on Aug. 5—8 159 trout of which 101 were fingerlings. Fishing with electricity does, however, with certainty not supply a quantitative value for the density of the population in the river, but is intended only to provide material on which an opinion about the composition of the stock in the rapids can be based. No char was caught in the rapids, but on the other hand 6 burbots.

Fishing in the pools (Aug. 13—18) as well as in Lill Korsvattnet shows the trout to be dominant also here, whereas the catch included only some single chars and burbots. In Lake Rensjön on the contrary the char are more numerous than the trout.

Table 2. Number of fish captured in Rensjöån and Lake Rensjön in the year 1955.

Locality	Trout	Char	Burbot
Rapids, El-fishing	159	—	6
Pools, Gillnets	42	1	2
Lill Korsvattnet, Gillnets	50	2	2
Rensjön, Gillnets	130	244	12

Table 3. Maturity of trout from Övre Rensjöån and Lake Rensjön in the year 1955.

Locality		Stage of maturity					
		I	II	III	IV	V	VI
Lill Korsvattnet	♂♂	18	4	—	2	—	—
	♀♀	16	8	1	—	—	—
Pools	♂♂	17	1	—	—	—	—
	♀♀	20	—	1	—	—	—
Fishway: young fish	♂♂	22	—	—	—	—	—
	♀♀	14	—	—	—	—	—
Spawning run up	♂♂	—	—	3	6	—	—
	♀♀	—	—	6	1	—	—
Spawning run down	♂♂	—	—	—	—	—	1
	♀♀	—	—	—	—	—	4
Lake Rensjön	♂♂	38	2	—	—	—	—
	♀♀	40	4	—	—	—	—

Maturity of the Rensjö Trout

The sexual maturity of the trout caught on the occasion of the test fishing during August 1955 in Lill Korsvattnet and in the pools was made the object of examination. In this year also random samples of the ascending fish in the ladder and of the descending and ascending spawning fish were taken. The result has been compiled in Table 3. The degree of maturity has been expressed by the figures I—VI, designating the following stages: I immature fish, II maturing fish, III and IV maturing fish expected to spawn in the same autumn, V mature fish ready to spawn, and VI spent fish.

The table shows that the trout ascending in the ladder, and which on account of external inspection had been designated as young fish were exclusively juvenile individuals. The descending spawning fish was in the stages III and IV, the males being slightly more developed than the females, while the five examined ascending fish were all in stage VI. Thus the distribution into young fish and spawning fish established in Table 1 ought on the whole to be correct.

Almost all the trout caught in the pools were juvenile individuals. Two trout had, however, started to develop the gonads, and were in stages II and III. In Lill Korsvattnet juvenile fish were in the majority, but a fairly large number of fish, males as well as females, were in stage II, while a female was in stage III, and two males in stage IV. Thus it seems as if some trout, both in the pools and in Lill Korsvattnet, could develop into mature fishes that might perhaps spawn in the autumn of the same year. As all migrating spawning fishes in the ladder and in the fence have been marked, it is excluded that the above mentioned fish could have descended from Rensjön or ascended from Korsvattnet.

The trout caught on occasion of the test fishing in Rensjön consisted for the greatest part of juvenile fish, only a minor portion being in stage II. The distribution in the catches of males and females is fairly equal (40 : 44).

During the entire period of observation (1947—1956) the sex of altogether 102 spawning trout descending in the ladder has been determined. Of these fishes 50 were males and 52 females. Thus the sex-ratio is close to 1 : 1. This sex-ratio does not agree with the findings of GUSTAFSON (1951) in the spawning run of trout in Dammån, where the females constituted 70 % of all ascending spawning fishes. ALM (1950) has found a predominance of females also in the sea-trout in the river Åvaån.

Age Composition of the Rensjö Trout

Fig. 6 gives a graphic representation of the age composition of the stock of trout in different parts of Övre Rensjöån and Rensjön. The statements about the age are based upon the number of year marks on the scale. Thus a fish in the first year of life belongs to age-group 0, one in its second year to age-group I etc.

The diagram shows clearly that different parts of the river are populated by different age-groups. In the rapids the fingerlings dominate, together with a small number of trout in the second and third year of life. Fishing with electricity also established a distinct difference between the dwelling places for age-group 0 and groups I—II. The fingerlings were encountered mainly near the flat portions of the shore with very shallow water and feeble current. The age-groups I and II, on the other hand, were caught especially in the main channel, where the water is deeper and the current faster.

The composition of the stock in the pools with their less agitated water is entirely different. There we find representatives of the age-groups II—VI with the youngest group in dominance. Age-group VI was represented by the female which was in maturity stage III (see above).

In the larger quiet water Lill Korsvattnet the trout is mainly in age-groups II—VII, the different age-groups being fairly uniformly represented. The age-groups II—V consist exclusively of juvenile fish, while the age-groups VI—VII contain a number of fishes in the maturity stages II—IV. The age-group VIII is represented by a single trout in maturity stage IV.

While thus only the younger fishes stay in the rapids, the older fishes seem to occur mainly in the more slowly flowing parts of the watercourse. This agrees with the distribution observed by SCHUCK (1943) for the brown trout in Crystal Creek, were the fingerlings, yearlings, and 2-years-old fish were more numerous in the fast running water than in the quiet water, and the 3-, 4- and 5-years-old fish were more numerous in the quiet water than in the rapids.

The juvenile trout ascending in the fish ladder in 1955 represented the age-

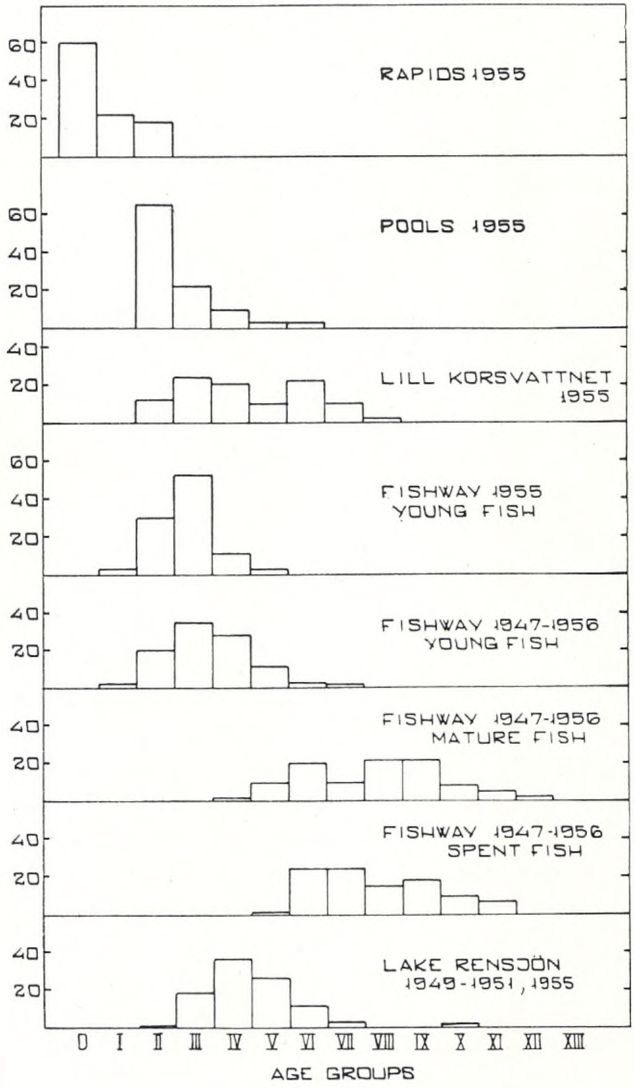

Fig. 6. Age composition of trout captured in different parts of the stream, in the fish ladder and in Lake Rensjön, expressed by percentage.

groups I—V, with the age-groups II and III in dominance. The average age distribution for the entire period 1947—1956 exhibits a similar picture, but during certain years the ascending fish has comprised a smaller fraction of older fish, representing the age-group VI—VIII. These older stages probably consisted of fishes which had begun to develop their gonads in the pools.

The mature trout descending from the lake to the river is composed of the age-groups IV—XII. The younger among these age-groups ought to represent faster growing individuals which have ascended to the lake at an early age. The age composition of the ascending spent trout is on the whole

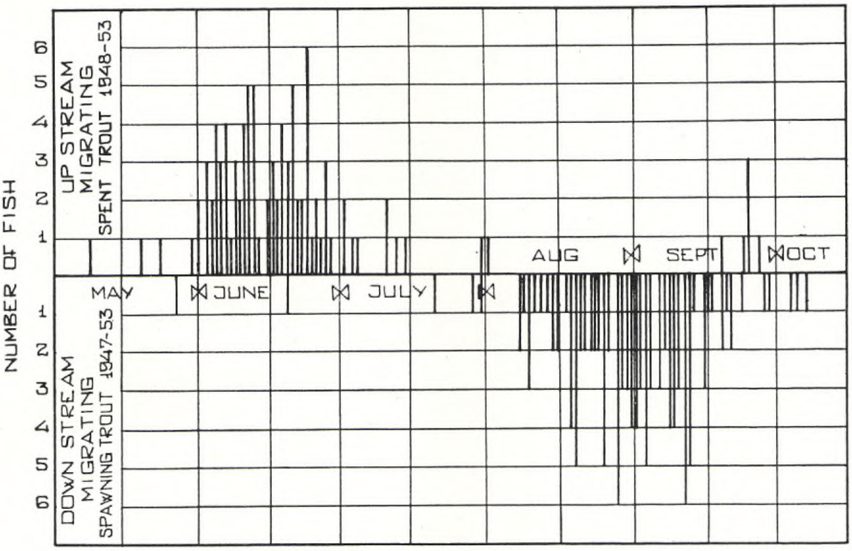

Fig. 7. The seasonal distribution of the spawning run in the fish ladder.

the same as that of the spawning fish, but seems to comprise a somewhat larger number of younger fish (age-groups VI—VII) than the descending.

Finally the age composition of the stock of trout in Lake Rensjön is shown on the basis of the test fishing in 1949—1951 and in 1955. Here we find a picture which reminds a good deal of the age composition of the young fish ascending in the ladder, but with a displacement by one year. While the age-groups II—IV dominate among the ascending fish, the catches from the lake are dominated by the age-groups III—V.

Migration of the Rensjö Trout

Spawning run

The descent of spawning fish to the river takes place mainly in August and September, as can be seen from Fig. 7. This downstream migration seems on the whole to be concluded during the first part of October. Single individuals can, however, descend also earlier in the summer.

Isolated individuals from among the spent trout can ascend to the lake in the autumn of the same year, after having passed 5—6 weeks in the river. The main mass of spent fish returns, however, to Lake Rensjön only in the following spring and summer, with the greatest intensity of migration falling into June and the first half of July.

The upstream migration of the Storsjö trout, that ascends for spawning in the river Dammån, takes according to GUSTAFSON (1951) place between the end of June and the end of September, with the maximum in July and August. No complete observations about the time of the descent are available, but two marked fishes caught during their descent in the beginning of October had stayed in the river 57 and 81 days, respectively. Thus in Rensjön, where the spawning places are situated in the outgoing river, the spawning run is more concentrated, and occurs later than in Storsjön, where the trout ascends into the river for spawning. In Dammån, however, the trout has to cover a very long distance in order to arrive at its spawning places in the upper reaches of the river, and experiments with marking have shown that fishes ascending in July spent 26—36 days upon a distance of about 12 kilometres.

During an inspection of Övre Rensjöån on Oct. 4, 1950 finished redds were observed along the entire length of the rapids, but even on Oct. 7 fishes ready for spawning could still be caught. On this occasion artificial fertilization of the roe was carried out. The main phase of the spawning ought to fall into the second half of September and the first half of October. Roe which had been fertilized in the first days of October 1947, and which had been exposed at the spawning places in cages hatched on May 6—10, 1948. Also roe dug up from redds in the autumn of 1947, and placed in cages hatched during the following spring (April 27—May 1).

Most of the spawning fish descending by the ladder into the river ought to spawn in Övre Rensjöån. Some trout, however, descend farther down the watercourse. During the time of function of the lower fence (cf. Fig. 2) 13 spawning trout descended in 1952 into Korsvattnet. Four of these trout had descended the same autumn in the ladder from Rensjön, and had been marked on this occasion. These fishes have probably spawned in the river below Korsvattnet. Three of these trouts then ascended the ladder in spent condition. Table 4 gives an account of spawning trout, marked in the fish ladder and recaptured in the lakes. The figure 0 indicates that marking and recapture have taken place in the same year, 1 stands for one year after the marking, 2 for two years, etc. Of the 69 marked ascending fish 5 have been recaptured in Lill Rensjön, while another 5 have made extensive migrations in Stor Rensjön, as can be seen also from the map in Fig. 1 in which also the recaptures of the spawning trout have been entered. Of particular interest in this connection is the fact that two fishes, which had descended once more in the river, have been recaptured in Korsvattnet below Övre Rensjöån, and one trout farthest down in Skärvattnet (cf. the map). Of the ascending fishes altogether 13 trout were caught by fishing, viz. about 19 % of the marked individuals.

Of the 88 mature trout marked in the ladder on their descent 5 have been

Table 4. Recapture of spawning trout marked in the fish-ladder 1947—1952.

		Lill Rensjön	Stor Rensjön	Kors-vattnet	Skär-vattnet	Laka-tjärn	total
Upstream migrating fish. N=69	0	4	1	—	—	—	5
	1	—	3	1	—	—	4
	2	1	—	—	1	—	2
	3	—	—	—	—	—	—
	4	—	1	—	—	—	1
	5	—	—	1	—	—	1
	total	5	5	2	1	—	13
Downstream migrating fish. N=88	0	—	—	—	—	1	1
	1	4	—	—	—	—	4
	2	1	1	—	—	—	2
	3	—	—	—	—	—	—
	4	—	—	—	—	—	—
	5	—	—	—	—	—	—
	total	5	1	—	—	1	7

recaptured in Lill Rensjön and 1 in Stor Rensjön after they had passed the ladder once more in upstream direction. Of particular interest is a male trout which had passed the ladder on Aug. 25, 1948 on its descent, and had migrated down the Övre Rensjöån to Korsvattnet. From there it had migrated upstream to Lakatjärn (cf. Fig. 1), where it had been recaptured on Aug. 31 of the same year. This trout would probably have spawned in the tributaries of Lakatjärn. Altogether 7 specimens or about 8 % of the descending trout were recaptured by fishing.

Thus the marking experiments show that the migratory area of Rensjö trout is not limited to Rensjön and Övre Rensjöån, but that the fish can descend also farther down in the drainage system, and that it can even ascend into the smaller tributaries.

In the course of the nine years of observation altogether 138 trout have been noted which moved downstream for spawning, and 131 trout, which ascended after the spawning to the lake. The figures given in the Table 1 for every year supply a fairly correct picture of the extent of the migration, with the exception of the years 1951 and 1952, when the grate in front of the dam gate had been removed during a certain part of the migratory season. It is not excluded that also isolated fish may have passed the ladder before or after the period of observation.

If we, however, compare in Table 1 the number of descending trout in the summer and autumn of one year with the number of ascending spent fish in the early summer of the following year, we meet with rather noticeable

Table 5. Recapture of marked down stream migrating spawning trout returning to Lake Rensjön.

Downstream migrating trout in the fish ladder				Upstream migrating trout returning to the lake						
				Number of marked fish recaptured					Number of unmarked fish	Total
				in the fishladder		in Lake Rensjön				
Year	Number of marked fish	Number of unmarked fish	Total	0	1	0	1	2		
1947	16	4	20	3	4	—	1	—	5	13
1948	34	—	34	—	10	—	—	—	14	24
1949	11	—	11	—	3	—	—	—	3	6
1950	15	—	15	—	9	—	—	—	7	16
1951	9	—	9	—	3	—	—	1	5	9
1952	3	1	4	2	3	—	—	—	18	23
Total	88	5	93	5	32	—	1	1	52	91

discrepancies. The number of ascending trout can be smaller than the number of descending fish during the preceding year, but also the reverse ratio can occur.

The first relation might be explained by the assumption that a number of fish have been caught after the downstream migration, or had died after spawning.

If, however, the ascending fish is more numerous than the descending, we must assume a contribution from waters farther down.

More light can, however, be thrown upon this problem by an analysis of the experiments with the marking of the trout descending in the ladder. Table 5 shows that from among the 93 trout which descended during the period 1947—1952 88 specimens were marked, while 5 remained unmarked. According to Table 4 none of these marked trout have been caught below Rensjön with the single exception of an individual caught in Lakatjärn. For this reason it might be expected that most of the marked descending fishes should be recaptured in the ladder on the ascent to Rensjön. This is, however, not the case. Only 37 of the marked descending trout have been recaptured in the ladder. Of these 5 ascended in the year of the descent, and 32 specimens in the following year. In Rensjön have furthermore been recaptured two marked trout which had escaped notice on the passage through the ladder. They have probably ascended outside the season of observations.

Thus altogether only 39 of the 88 descending trout have ascended again into Rensjön. In addition to them a total of 52 trout without marks has passed the ladder on its upstream way to Rensjön during the time of observation. These latter were marked before being let into the lake.

The possibility exists that some of the descending fishes have lost their marks during their stay in the river. In the sea trout in the river Åvaån ALM

Table 6. Recapture of marked upstream migrating spent trout returning as mature fish to the stream.

Marked upstream migrating spent trout in the ladder		Number of trout recaptured as downstream migrating mature fish in the ladder			
year	nr of fish marked	0	1	2	3
1947	7	3	2	—	—
1948	9	—	1	—	—
1949	23	—	4	—	—
1950	6	—	2	—	—
1951	16	1	4	—	1
1952	8	—	—	—	1
Total	69	4	13	—	2

(1950) found that about 50 % of the spawning fish lost their marks in the time which lapsed between their ascent and descent in the river. This could be established by the occurrence of distinct wounds after the marks. No such signs of earlier marking could, however, be established upon the 52 ascending fishes. There is also reason to suppose the employed marking method to have been reliable, since marked fish have been recaptured as late as 5 years after the marking, as can be seen in Table 4.

The conclusion seems therefore unavoidable that not all spawning fishes descending from Rensjön return to the lake, but that a new supply of spent fish from farther downstream situated watercourses takes place instead. As we have seen already above, some spawning trout from Rensjön can descend rather far down in the watercourse, and some of these fishes ought to stay in the small lakes of this region. Table 1 shows, on the other hand, that spawning trout ascends from Korsvattnet and Lill Korsvattnet to Övre Rensjön. Part of this trout presumbly ascends to Rensjön after spawning.

It is worthy of interest that part of the new supply of trout which has apparently ascended from the lakes lower down in order to spawn in Övre Rensjöån, and which afterwards has ascended still farther to Rensjön, has after some years descended into Rensjöån in order to spawn there once more. Thus one of the recently marked trout which ascended in the ladder on June 23, 1948 has again descended to Övre Rensjöån on Sept. 11, 1949, in order to return to Rensjön on June 27, 1950. After this it has again migrated right down to Korsvattnet, where it was caught on May 27, 1953. During the following years 7 individuals of such recently marked fish have again descended into the river one or two years after their ascent.

Thus it seems as if one and the same fish could both ascend and descend for spawning. This is supported also by the first-mentioned spawning trout which first descended from Rensjön to Korsvattnet, and then ascended to Lakatjärn.

Table 6 shows, how long time the ascending spent fish stays in Rensjön before it again descends into the river for spawning. Table 4 shows that during the period 1947—1952 of the 69 marked trout which had spawned in the autumn of the preceding year 13 individuals have been recaptured. Nineteen of the remaining trout have returned in order to spawn once more (Table 6). Of these 4 trouts have returned into the river in the same year in which they had ascended, and have thus spawned again one year after the preceding spawning. Thirteen specimens have stayed in the lake for another year, and have descended two years after the preceding spawning. A single trout has descended only after four years in order to spawn again. This agrees fairly well with the results of ARVIDSSON's marking experiments (1935) with the trout from Vättern. Of 42 recaptured trout 11 specimens spawned with an interval of 1 year, 20 individuals after 2 years, 7 individuals after 3 years, 3 individuals after 4 years, and 1 individual after 5 years. In both populations of trout the majority of fishes have spawned with an interval of two years.

Of the marked trout which have spawned more than once only one individual has been observed to have spawned three times. This was a 68 cm. long female which had been marked on its ascent in the ladder on July 1951, and which had then been recaptured on its renewed ascents on June 3, 1953 and on July 8, 1955. The size of this trout, which thus spawned in the autumns of 1950, 1952, and 1954, makes it probable that it had spawned already earlier one or several times.

Of the young fish which had grown up in Övre Rensjöån, and which had ascended into the lake for the first time, when it was marked in the ladder, two trouts have returned during the period of observation to the river in order to spawn for the first time. One of them ascended in July 1949, and had then a length of 33.5 cm. In Aug. 1952 it descended in the ladder, when it had reached a length of 39 cm. In the following June it returned to Rensjön. The other trout ascended in July 1951, when it was 27 cms. long, and returned to the river in Sept. 1952. After a stay in the lake of slightly more than a year it had then reached a length of 35 cm. It returned to Rensjön in June 1953.

The run of juvenile trout

As is demonstrated in Table 1 the migration of young fish is directed mainly upstream towards Rensjön, and the few individuals which descended are preponderantly fish which had first ascended to the lake, but which soon afterwards has returned to the ladder, perhaps passively carried there by the current.

Fig. 8 illustrates the extension of the migratory seasons during the years 1949, 1951, 1953, and 1955. Every pile symbolizes the number of ascending trout *per diem.* The figure contains in addition a curve which shows the dayly changes of the temperature of the water during the period of observation. Daily determinations of the temperature have been carried out at 8.00

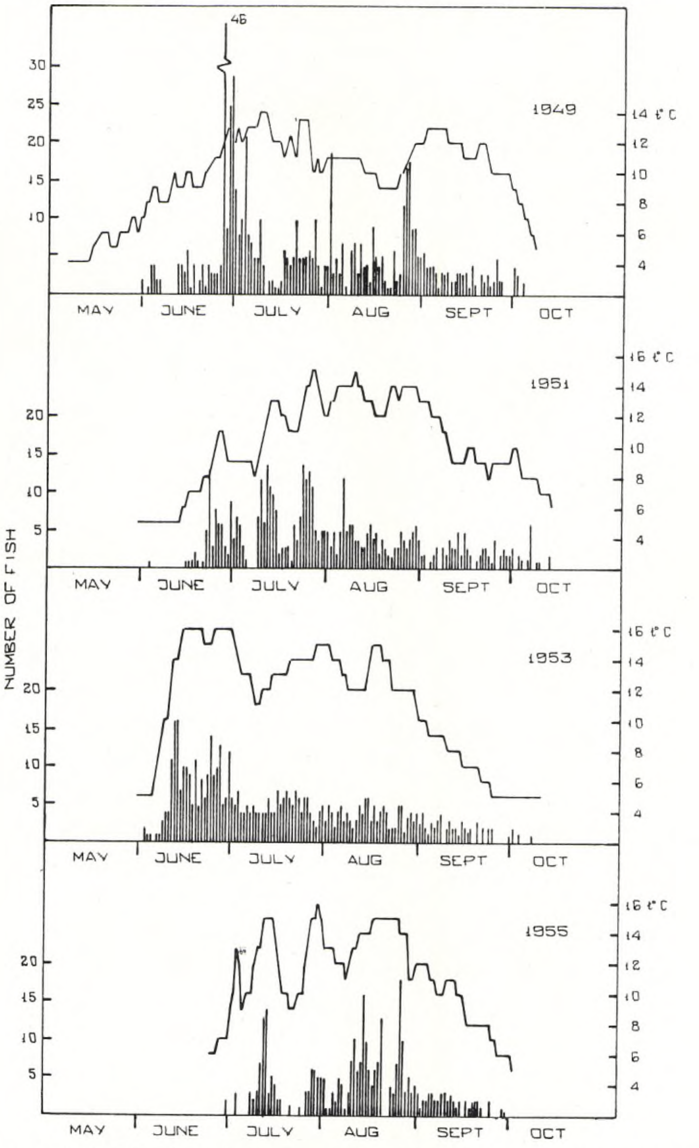

Fig. 8. The seasonal distribution of the up-stream migration of the young fish in the fish ladder and the fluctuations of the water temperature in the stream.

a.m. in the river below the dam. As already pointed out the amount of flow in the river has been fairly constant throughout the time of migration, being between 1 and 2 m^3/sec. This constancy is due to the regulation of the lake.

The migration seems to start only after the ice of Rensjön has opened, and the temperature of the water has started to rise. This usually happens during the first days of June. In this respect agreement exists with MOTTLEY's observations (1938) about the intensity of the spawning run of the rainbow trout in Lake Paul, where it is definitely associated with the warming up of the water both in the lake and in the creek during the first spell of bright, clear, settled weather in spring after the ice has left the lake.

The termination of the migration usually falls into the first days of October, when the temperature of the water is falling considerably. As a general statement we can say that the migration of the trout is restricted to the time, while the temperature of he water exceeds 5—6°C.

The migration seems, however, to be particularly stimulated by quick rises in temperature, probably through an increase of the activity of the fish. Every rise of temperature is coupled with a rush in the upstream migration, as can be seen clearly in the diagrams in Fig. 8, whereas a stagnation can often arise after the reaching of a maximum temperature. Also for *Salvelinus fontinalis* ELSON (1942) has established by experiments that the amount of movement of a trout resulting from a given stimulus increases with increasing temperature up to about 10°C. This temperature lies below the halfway point between the upper and lower temperature limits of the animal. Above about 10°C further increases of temperature have the opposite result. BROWN (1946) has found also in brown trout a maximum activity at 10—12°C.

On account of the dependence of the migratory activity on the temperature the peaks of upstream migration arrive at rather different times in different years, depending on the temperature conditions (cf. Fig. 8). Thus in 1949 a fast rise of temperature from 9° to 13°C caused the maximum ascent to fall round the turn from June to July. This was followed by a short period of stagnation in spite of the fact that the highest temperature of the year was reached some days later. Another rush took place at the end of August, when the temperature again rose rapidly from 9° to 13°C.

During the year 1951 a number of fast rises of temperature amounting to 4—5°C with following drops in temperature were registered during June and July, and every rise of temperature is seen to be followed by a rush in migration. For this reason the main part of the ascending migration fell into these two months, the activity decreasing during the later part of the season.

The years 1953 and 1955 exhibit particularly great contrasts. In 1953 June was warm and sunny, and the first part of this month shows a very fast rise in the temperature of water from 5° to 16°C with an ensuing lively activity of the fish. In 1955, on the other hand, the temperature of June was very low, and no greater activity of the trout could be observed before July, when the temperature started to rise. In this year the most intense ascent took place during the month of August.

A great part of the young fish which passed the fences and the fish ladder has been marked. In this connection it is of interest to see to what extent the fishes which have passed the upper and lower fence (cf. the map, Fig. 2) take part in the migration in the fish ladder. The result of the marking experiments in the fences has been accounted for in Table 7.

The upper fence at the outflow of Övre Rensjöån into Lill Korsvattnet has been functioning only during a short time in 1955, but functioned during the greater part of the migratory season of 1956. During this years 86 ascending and 13 descending juvenile trout have been marked. Twelve of the ascending fishes descended again in the same summer, and two other trouts were recaptured in the lower fence on their descent to Korsvattnet. Only two of the 86 marked trout have been recaptured in the fish ladder on their way to Rensjön.

Of the 13 descending trout 1 continued down to the lower fence, while two fishes turned round and re-ascended into the upper fence, whereupon one of them returned to Lill Korsvattnet.

Thus the migration of the trout between Lill Korsvattnet and the reach of the river above it seems to consist mainly of short rushes between quiet water and rapids, and few fishes only have migrated right up to Rensjön. The fish which ascends to Rensjön through the fish ladder must, therefore, be recruited mainly from the pools and rapids above Lill Korsvattnet.

At the lower fence mainly a descent to Korsvattnet takes place, as has already been pointed out in Table 1. This was the case especially in the years 1952 and 1953. During the years 1955 and 1956, when the fences were set up later in the season, the migration was of much smaller extent. In 1952 and 1953 altogether 43 ascending and 303 descending trout have been marked (Table 7). Seven of the ascending fishes returned to Korsvattnet in the same or in the following summer. From among the descending trout only a small percentage (18 individuals) returned to Lill Korsvattnet during the summer 1952 and 1953, while 5 fishes ascended still farther to Rensjön, and were recaptured in the fish ladder. The majority of the descending trout stayed, however, in the lower watercourses, and has spread there far down into the river, as is testified by recaptures in Korsvattnet, Skärvattnet, Summulsjön, and Vukumaån.

Part of the trout growing up in Lill Korsvattnet ought to form a stationary stock, and we have seen already earlier that the trout can develop there into mature fish. Of the emigrating trout only an inconsiderable number goes to Rensjön, while the major part descends into Korsvattnet and the lakes below it.

In the time from 1947—1951 3300 young fish have ascended in the fish ladder, and of these 1324 have been marked, as can be seen from Table 8. Of these marked fishes altogether 17 individuals have redescended into the river, and the 1307 trout which have remained in Rensjön have there been the object of fishing. In this way 152 trouts or 11.7 % of all marked fishes have been recaptured in Lill Rensjön, as against only 42 specimens or 3.1 % in Stor Rensjön. Thus altogether 14.8 % of the marked fishes have been ob-

Table 7. Recaptures of young trout marked in upper and lower fences.

Marked young fish				Recaptures of marked fish										
Locality	Year	Direction of migration	Number of fish	Year	Lower fence		Upper fence		Fish way		L. Korsvattnet	L. Skärvattnet	L. Summulsjön	R. Vukumanån
					up	down	up	down	up	down				
Upper fence	1956	up	86	1956	—	2	—	12	2	—	—	—	—	—
»	1956	down	13	1956	—	1	2	1	—	—	—	—	—	—
Lower fence	1952	up	12	1952	—	2	out of function		—	—	—	—	—	—
				1953	—	1			—	—	—	—	—	—
»	1952	down	153	1952	3	—			—	—	2	—	—	1
				1953	2	5			5	—	2	—	—	—
				1954	—	—			—	—	—	1	—	—
»	1953	up	31	1953	—	4			—	—	—	—	—	—
»	1953	down	150	1953	13	1			—	—	—	1	1	—

Table 8. Recaptures of up-stream migrating young trout marked in the fish ladder.

Year	Total number in the ladder	Number of fish marked	Returning to the ladder	Remaining in the lake	Lill Rensjön						Stor Rensjön						Total	Recaptures in per cent
					0	1	2	3	?	Total	0	1	2	3	?	Total		
1947	652	200	1	199	9	1	—	—	1	11	—	1	—	—	—	1	12	6.0
1948	1024	303	12	291	27	20	1	1	—	49	—	4	5	—	1	10	59	20.1
1949	582	282	—	282	11	18	1	1	—	31	2	7	2	1	—	12	43	15.1
1950	595	266	3	263	32	4	2	—	—	38	7	3	2	—	—	12	50	19.1
1951	447	273	1	272	15	8	—	—	—	23	2	5	—	—	—	7	30	11.0
Total	3300	1324	17	1307	94	51	4	2	1	152	11	20	9	1	1	42	105	14.8

Table 9. Estimation of the size of the trout population in Lill Rensjön based on marking experiments.

Year	Date of test fishing	Number of trout marked in the same season present in the lake	Number of captured trout		Estimated size of the population
			Total	Marked in the same season	
1949	July 16—22	158	59	7	1,322
1950	Aug. 6—9	203	159	29	1,113
1951	Sep. 4—9	219	75	15	1,095

tained by fishing, indicating a low intensity of this activity. A fairly large part of the recaptures has been made on occasion of our own test fishing. Since the intensity of the fishing can be assumed to be fairly the same in the two lakes, the marking experiments can be interpreted as indicating that the major part of the ascending trout stays in Lill Rensjön.

Table 8 shows that the largest number of marked fishes, viz. 94 individuals, has been caught in Lill Rensjön already in the same year in which the fish had ascended into the lake. During the three following years 51, 4, and 2 trouts, respectively, have been caught; this is indicative of a fairly high mortality in the lake.

In the year in which the marking had been carried out only 11 trouts have been caught in Stor Rensjön, whereas the greatest number, viz. 20 individuals, was caught only in the year following the marking. Thus the spreading from Lill Rensjön to Stor Rensjön takes place at a fairly slow rate.

Whereas the ascending spent fish spreads more uniformly over the whole of Rensjön, the young fish ascending from Övre Rensjöån seems to invade mainly Lill Rensjön, and only to a smaller extent to spread also to Stor Rensjön. Thus the stock in Stor Rensjön must be recruited to a large extent from fish growing up in the feeding brooks.

In Table 9 the stock of trout in Lill Rensjön has been calculated on the basis of the marking experiments according to the simple presupposition that the ratio between the number of recaptured fish to that of caught fish is the same as the ratio between the total number of marked fish to the number representing the total stock of the lake. For each of the years 1949, 1950, and 1951 the Table contains the number of fishes marked during the summer next to the dates for the test fishing. It also includes the number of trout caught during the different test fishings, and how many among them represent recaptures of fishes marked during the course of the same summer.

The Table shows the stock in Lill Rensjön to have fluctuated between about 1100 and somewhat more then 1300 trout during the period of examination. With the area of Lill Rensjön being 297 hectares (=c. 730 acres) the density of the stock is only 4—5 individuals per hectare, thus very low. As has already been said, the char is, however, the dominating fish in the lake.

Migration of the Char

From Table 1 can be seen that during the years 1947—1956 699 chars have been caught in the fish ladder on their way up to Rensjön, while only 19 fishes were downstream bound. As in the cases of the trout some of these latter had ascended earlier to the lake, but soon afterwards returned to the ladder.

The char occurs in all lakes of the drainage system, but is scarce both in Övre Rensjöån and in Lill Korsvattnet, as is evident from the results of the test fishings accounted for in Table 2. Thus the ascending char must be derived from Korsvattnet or from the lakes immediately below it, and must only pass Övre Rensjöån on its way to Rensjön without staying there for any length of time.

The time of migration extends over the entire summer in the same way as with the young trout. In difference from the trout the ascending char is, however, represented by adult fish, a great part of which is due to spawn in autumn. During the year 1955 a determination of the sex has been carried out on a smaller number of chars which had been caught in the fish ladder; this is accounted for in Table 10. Of 24 examined fishes half were males and half females. Most of the ascending chars have developed gonads. This maturity was the more advanced, the later in the season the fishes were caught, and 2 males and one female, caught in September, were ready for spawning (stage V).

Also the migration of the char after its ascent into Rensjön differs from that of the immature trout, as can be seen from Table 11. Of the 443 marked char which stayed in the lake during the period 1947—1951 altogether 63 individuals or 14.2 % have been recaptured; this closely corresponds to the recaptures established in the case of the trout. The distribution of the recaptures upon Lill Rensjön and Stor Rensjön is, however, entirely different. The greatest number of char, viz. 47 individuals or 10.6 %, was recaptured in Stor Rensjön, and most of them, viz. 31 individuals, were recaptured in the year of their ascent. The char does not, like the greater part of the ascending trout, stay in Lill Rensjön, but moves rather quickly to Stor Rensjön, and has been caught there mainly on the occasion of the fishing in autumn which takes place at the spawning grounds of the char about 10—12 kms. above the dam. Thus 24 of the 31 chars, recaptured in Rensjön in the year of their ascent, were fished upon the spawning grounds of the char during September and October. Of the 8 recaptured in the year following the marking 4 were obtained during the fishing for spawning char, and of the 6 recaptured 2 years after the marking two were taken during the spawning season. One of the chars ascending in the ladder has also moved from Lill Rensjön farther upstream to Stortjärn (cf. the map, Fig. 1).

A similar migration of the char has been observed by FABRICIUS (1950) in Lake Stor Sjouten. Following upon the damming-up of this lake a number of

Table 10. Maturity of char captured in the fish ladder in the year 1955.

Sex	Stage of maturity						Total
	I	II	III	IV	V	?	
males	2	3	1	2	2	2	12
females	—	2	3	5	1	1	12

obstacles to migration in affluent brooks in the shape of steeper passages came below the damming level, and a free passage was opened for the fish. FABRICIUS was able to observe that during its spawning time the char ascended into tributaries, where it had not spawned before. The longest migration was performed in the 4 kms. long river Gransjöån up to a lake Lill Sjouten, where previously only trout had occurred.

The char is obviously a migratory fish to a larger extent than had hitherto been assumed, and seems first of all to exhibit a tendency towards an ascent into more elevated lakes, provided that its ways is not closed by obstacles preventing its migration. The char being a fish thriving in cold water, the stock ought to benefit from a spreading into more highly situated and colder lakes.

Recruitment and Survival of the Trout Population in Lill Rensjön

As pointed out in the foregoing the recruitment of the stock of trout in Lill Rensjön is effected mainly by the ascent of young fish from Övre Rensjöån. Table 12 gives the numbers of ascending young fish for every year during the periods 1947—1953 and 1955—1956, distributed over age-groups.

The most intense upstream migration took place during the first part of the period, and culminated in 1948 with more than 1000 fishes. During the later part of the period the number of ascending fishes lies below the average for the entire period of observation. These conditions depend on fluctuations in the strength of year-classes which shall be dealt with later.

The number of ascending fishes was on the average 550 individuals, produced mainly in the about 650 m long stretch of the river between Lill Rensjön and Lill Korsvattnet. The average for descending spawning fish is 19, if we disregard the years 1951, 1952, and 1956, when some fish could descend through the dam gate without being checked. Half the number of these fishes or about 10 individuals *per annum* were females.

The ascending fishes represent the age-groups I—VIII. Among them dominate fishes of the mean age of 3 and 4 years, after these come individuals of 2 and 5 years, and 6 years and 1 year. The age-groups VII and VIII are very feebly represented. As already pointed out (Table 3) the older fishes in the pools of Rensjöån and in Lill Korsvattnet had already begun to develop their gonads, and a certain percentage of maturing fish is included probably also among age-groups VII and VIII.

On the basis of the years spent in the river, which in certain cases can be counted upon the scales, ALM (1929) has calculated that the Vättern trout ascends to the lake from the river Motala ström at the age of 1—5 years, with a maximum upstream ascent in the females of 2 or 3 years' age, thus somewhat earlier than in the Rensjö trout. According to HUITFELDT KAAS (1927) the commonest age of emigration for the trout of Norway is said to be after 3 years' stay in the river, thereafter comes 4 years, then 2 years and at last 5 years. The trout very seldom stays in the river for 6 years, and a stay of 7—10 years seems to be altogether exceptional. Also in the trout of lake Mjösen DAHL (1910) has established on the basis of the zones of growth of the scales that the descent into the lake takes place most usually at the age of 5 years, thereafter at 4, 6, and 3 years of age. There seems to exist no essential difference with regard to the age of emigration between trout which grows up in the outlet, and then ascends into the lake (Vättern and Rensjö trout), and trout growing up in the tributary river (Mjösen trout), and ascending then into the lake.

In Rensjön the age of ascent of the trout can vary from year to year with a maximum at 3, 4, or even 5 years' age. This can depend in part on the fluctuations in the year-classes, but also other contributary causes may exist.

Observations of the ascent in the fish ladder have supplied us with informations about the recruiting of the stock of trout in the lake from the river over a longer period of time. The number of fish belonging to the various age-groups in a population may be used for the estimation of the percentage of fish that survive from one year to the next according to JACKSON's (1939) formula $S = \frac{x_2 + x_3 + x_4 + \ldots x_n}{x_1 + x_2 + x_3 + \ldots x_{n-1}}$.

On the basis of the age distribution of the trout in the lake (Table 13) the survival of age-groups IV to V after the ascent from the lake has been calculated as 72 %. The survival of age V to age VI was 44 %, the survival from age VI to VII 29 %, and the survival from age VII to age VIII 18 %. The average annual survival of all age groups from IV—VIII was 54 %, and the average annual mortality thus 46 %. The average survival of all age groups from V—VIII was 38 %, and the average mortality 62 %. In wild brown trout in Crystal Creek SCHUCK (1945) found an average annual survival of all ages amounting to 36.1 %, and NEEDHAM, MOFFET, and SLATER (1945) calculated the average over-winter survival of wild brown trout in a California river to 40.0 %. These figures agree with the average survival of the older age groups V—VIII of the Rensjö brown trout.

SHETTER and LEONARD (1942) found the survival of brown trout in Michigan trout stream to be 65.9 % between the first and the second summer, 64.3 % between the second and the third, and 13.7 % between the third

Table 11. Recaptures of upstream migrating char marked in the fish ladder.

Year	Total number in the ladder	Number of fish marked	Returning to the ladder	Remaining in the lake	Recaptures												Total	Recaptures in per cent
					Lill Rensjön						Stor Rensjön							
					0	1	2	3	?	Total	0	1	2	3	?	Total		
1947	94	76	—	76	—	2	—	—	—	2	5	1	—	—	—	6	8	10.5
1948	124	106	1	105	4	2	1	—	1	8	8	1	—	1	—	10	18	17.2
1949	79	75	—	75	—	2	—	—	—	2	7	3	1	—	—	11	13	17.3
1950	103	82	—	82	2	—	—	—	—	2	7	1	1	1	—	10	12	14.7
1951	107	105	—	105	1	1	—	—	—	2	4	2	4	—	—	10	12	11.4
	507	444	1	443	7	7	1	—	1	16	31	8	6	2	—	47	63	14.2

Table 12. The observed number of upstream migrating young trout in the fish ladder in the period 1947—1956 separated in age groups.

Calender-year	Age groups								Total
	I	II	III	IV	V	VI	VII	VIII	
1947	29	136	128	263	55	16	16	9	652
	4.5	20.8	19.6	40.3	8.5	2.4	2.4	1.4	99.9 %
1948	72	180	233	198	269	36	18	18	1024
	7.0	17.6	22.8	19.3	26.3	3.5	1.8	1.8	100.1 %
1949	5	163	216	134	43	16	5	—	582
	0.9	27.8	37.1	23.1	7.4	2.8	0.9	—	100.0 %
1950	—	101	239	119	110	18	9	—	596
	—	16.9	40.0	20.0	18.5	3.1	1.5	—	100.0 %
1951	—	—	64	223	112	32	16	—	447
	—	—	14.3	50.0	25.0	7.1	3.6	—	100.0 %
1952	—	24	129	268	35	24	—	—	480
	—	4.9	26.8	56.1	7.3	4.9	—	—	100.0 %
1953	—	55	87	246	76	22	17	—	503
	—	10.9	17.4	48.9	15.2	4.4	3.3	—	100.1 %
1955	10	96	164	36	10	—	—	—	316
	3.3	30.1	52.0	11.3	3.3	—	—	—	100.0 %
1956	13	73	226	33	—	7	—	—	352
	3.8	20.8	64.1	9.4	—	1.9	—	—	100.0 %
	129	828	1486	1520	710	171	81	27	4952
	2.6	16.7	30.1	30.7	14.3	3.5	1.6	0.5	100.0 %

and the fourth summer. Gupp (1955) found also in a brook trout population in Sunkhaze values for survival which strongly dropped with increasing age. The survival of age groups II—III was 48.3 %, of age groups III—IV 21.7 %, of age groups IV—V 16 %, and of age groups V—VI 12.5 %. The average annual survival of all age groups above I was 37.8 %.

Allen (1951) found the survival of brown trout in Horokiwi stream to be 28 % over a full year in earlier life, and 17 % in the remainder of the life.

Kennedy (1954) has estimated the mortality of an unexploited lake trout population in Great Slave Lake. The annual mortality rate was about 33 % at 10 years' age, 39 % at 15, and 49 % at 20 years. The average annual mortality of age groups IV—VII of the Rensjö trout was 46 %. According to the marking experiments (Table 8) about 15 % of the ascending young fish are caught during the first four summer after the ascent. Thus the average mortality due to causes other than fishing ought to be about 31 % for age groups IV—VIII.

On the basis of the calculated percentage of survival for the different age groups the fate of any individual year-class can be followed after its ascent to the lake. In doing so the author has calculated for the younger age groups with the same survival as for the age groups IV—V, viz. 72 %. The diagonal rows in Table 12 supply the number of ascending trout in every individual year-class, distributed over the different age groups. Complete information is available for the year-classes 1946, 1947, and 1948 of which 697, 754, and

Table 13. Age composition of trout from Lake Rensjön captured by gillnets in the years 1949, 1950, 1951 and 1955.

Age groups										
I	II	III	IV	V	VI	VII	VIII	IX	X	Total
1	4	61	119	86	38	11	2	1	3	326
0.3	1.2	18.7	36.7	26.4	11.7	3.4	0.6	0.3	0.9	100.2

514 fishes, respectively, have ascended to the lake. Table 14 shows, how initially the number of fish in the lake increases through the annual recruitment from the river, and how it reaches a maximum at age V for the year-class 1946, and at age IV for the year-classes 1947 and 1948. Subsequently the increasing mortality causes a rapid drop in the number of fish, and at age IX only single fishes are left. It is therefore understandable that large fishes are relatively rare, and that trout descending for spawning are rather few, especially since the Rensjö trout spawns as a rule every other year only.

The annual recruitment to the lake from Rensjöån distributed over different age-groups (Table 12) and the survival of the different age-groups being known, we are able to calculate the magnitude of the stock which is produced by the ascending trout at a given time. In Table 15 the magnitude of the stock of the year 1953 has been calculated on the basis of the recruitment during the years 1947—1953. It appears from the Table that from among the 652 fishes which ascended in 1937 only 2 specimens are left in age-groups VII and VIII. Of the trout ascended in 1948 only 5 fishes remain, distributed over the age-groups VII—IX, etc. In 1953 the lake contained altogether 1106 trout, derived from Rensjöån, and distributed over the age-groups II—IX.

This figure agrees well with the values for the size of the stock in Lill Rensjön which had been obtained on the basis of the marking experiments.

The distribution over the different age-groups exhibits a fairly good agreement with the age distribution of the trout caught in Rensjön in the years 1949—1951 and 1955 on occasion of the test fishings (Table 13). In either case the age-groups IV and V show the strongest representation.

Table 15 contains also the total weight of the trout of different age-groups. The calculations are based upon the average weights of different age-groups

Table 14. Number of trout of the year classes 1946, 1947, and 1948 present in the lake at different age.

Year class	Age groups								
	I	II	III	IV	V	VI	VII	VIII	IX
1946	29	201	361	379	437	192	56	10	2
1947	72	215	393	506	399	175	51	9	2
1948	5	105	140	369	341	150	44	8	1

Table 15. The estimated size of the trout population in the Lake Lill Rensjön in the year 1953 based on the recruitment during the period 1947—1953 and the calculated mortality.

Recruitment		Number of survived trout in the lake in the year 1953									
Calendar year	Number of fish	Age groups I	II	III	IV	V	VI	VII	VIII	IX	Total number
1947	652	—	—	—	—	—	—	1	1	—	2
1948	1024	—	—	—	—	—	—	2	2	1	5
1949	582	—	—	—	—	1	27	14	2	—	44
1950	596	—	—	—	—	38	55	11	2	—	106
1951	447	—	—	—	—	33	71	14	2	—	120
1952	480	—	—	18	93	193	15	7	—	—	326
1953	503	—	55	87	246	76	22	17	—	—	503
Total		—	55	105	339	341	190	66	9	1	1106
Percent		—	5.0	9.5	30.7	30.8	17.3	6.0	0.8	0.1	100.2
Weight kg		—	5.1	11.3	57.7	90.8	88.2	45.2	7.4	1.2	306.9

as given in Table 22.. It becomes apparent that the age groups V and VI account for the greatest amount by weight, representing together 58.3 % of the total weight of the stock which is 306.9 kgs.

The Calculated Growth of the Rensjö Trout

In the Tables 16—19 has been shown the calculated growth of year-classes of trout captured as mature descending fish in the fish ladder, of trout captured in the lake with gill-nets, and of immature ascending trout passing the fish ladder. In Fig. 9 the calculated general growth and the increment in length of the three categories of trout are given.

Table 16. Calculated growth in length of year classes of mature downstream migrating trout captured in the fish ladder.

Year class	Number of fish	Calculated length (mm) at the end of year of life 1	2	3	4	5	6	7	8	9	10	11
1937	2	71	102	162	213	266	341	398	444	524	583	617
1938	3	64	121	168	233	306	428	503	572	611	656	630
1939	9	70	127	200	272	407	466	540	592	616	—	—
1940	5	64	110	159	218	278	378	414	512	548	581	—
1941	3	67	118	202	280	361	444	491	544	571	—	—
1942	7	60	112	181	253	339	420	488	578	654	688	—
1943	10	71	119	186	244	311	350	375	383	—	—	—
1944	3	51	98	151	201	290	319	352	—	—	—	—
1945	5	53	107	173	256	321	348	—	—	—	—	—
1946	2	60	117	174	232	297	278	306	—	—	—	—
1947	2	61	117	180	248	317	388	—	—	—	—	—
Average length		63	113	176	241	318	378	430	518	587	627	624
» increment . .		63	50	63	65	77	60	52	88	69	40	—

Table 17. Calculated growth in length of year classes of trout captured by gillnets in Lake Rensjön in 1949—1951 and 1955.

Year class	Number of fish	Calculated length (mm) at the end of year of life									
		1	2	3	4	5	6	7	8	9	10
1941	2	62	122	201	270	357	457	541	612	662	700
1942	3	57	109	171	229	290	350	415	471	—	—
1943	12	51	103	155	210	268	320	396	—	—	—
1944	32	54	103	157	213	271	338	400	—	—	—
1945	62	55	111	173	227	287	342	—	—	—	—
1946	28	56	118	183	239	306	—	—	—	—	—
1947	18	56	123	186	251	—	—	—	—	—	—
1948	10	59	124	184	227	304	386	460	—	—	—
1949	8	62	117	170	222	285	353	—	—	—	—
1950	23	57	110	168	229	298	—	—	—	—	—
1951	32	56	113	176	241	—	—	—	—	—	—
1952	19	60	132	202	—	—	—	—	—	—	—
Average length		57	115	177	233	296	364	442	541	662	700
» increment ...		57	58	62	56	63	68	78	99	121	38

As no determination of the sex was possible of the fish passing the fish ladder, the study of the growth for either sex has not been possible. According to Alm (1929), however, the increase of size is about equal in either sex in the Vättern trout. Also Huitfeldt Kaas (1927) points out that this difference is inconsiderable between the males and females of the trout in Norwegian lakes.

The diagrams representing the growth of the trout caught in Rensjön in summer and that of the descending spawning fish exhibit a fairly good agreement, and the discrepancies in length shown for the older age groups ought to be due to the scarcity of material from these groups.

Table 18. Calculated growth in length of year classes of immature upstream migrating trout captured in the fish ladder.

Year class	Number of fish	Calculated length (mm) at the end of year of life						
		1	2	3	4	5	6	7
1942	11	62	113	166	221	253	325	372
1943	51	59	111	158	205	255	336	364
1944	39	58	107	156	208	269	316	—
1945	68	60	113	173	226	270	285	—
1946	78	58	113	174	228	293	326	362
1947	81	66	133	186	240	282	325	364
1948	58	64	123	183	240	275	322	369
1949	67	55	115	173	226	267	317	—
1950	22	60	124	183	217	269	316	—
1951	24	56	116	176	240	—	—	—
1952	68	52	116	175	216	—	—	—
1953	112	54	117	158	—	—	—	—
Average length		59	117	172	224	270	318	366
» increment		59	58	55	52	46	48	48

Table 19. Calculated growth in length of trout from the rapids 1955 (el-fishing).

Year class	Number of fish	Calculated length at the end of year of life 1	2	3	4	5
1954	10	51	—	—	—	—
1953	8	54	101	—	—	—
Average length		53	101	—	—	—
» increment		53	48	—	—	—

During the earliest years of life we also find good agreement in the growth between the trout which has been living in the lake and the fish about to ascend from the river. Starting, however, from the third year of life the fish in the river exhibits a much poorer growth than the trout caught in the lake. This becomes particularly noticeable on comparison of the annual increment in length of the two categories.

While in the river trout the increment in length decreases with age, the trout from the lake exhibits a strongly increasing annual increment in length which is somewhat irregular, but which on the whole increases with growing age. This difference in growth ought to be caused by the fact that, after ascending into the lake the trout finds itself in a more favourable nutritional environment. NILSSON (1957) who has studied the collected samples of stomach contents of the Rensjö trout has shown the trout caught in the lake to feed to a large extent on fish, while in the river the fish diet plays a subordinate rôle, and occurs only to a minor extent in the pools of the river and in Lill Korsvattnet with its feeble current.

In spite of this increase in growth after the ascent into the lake the Rensjö trout is not seen to possess upon its scales the sharp boundary between "river years" and "lake years" which has been described for some forms of trout, and which is particularly evident in the sea trout and the salmon. For this reason it is not possible to count with certainty the "river years" upon the scales of the Rensjö trout. According to HUITFELDT KAAS this is the case also in most forms of trout examined by him from Norwegian lakes.

Also upon the river stage the trout exhibits a strong variation of growth which depends not only on individual competition, but which ought to be connected also with the food supply in the different habitats of the river. The different age stages dwell in the river in different habitats, as has already been pointed out (cf. Fig. 6). Thus the fish which is only one summer old stays in the shallower portions of the rapids, where the current is feebler. In the stronger current mainly fish in the second and third summer is encountered, while the older fish stays in the pools with fairly feeble current.

Tables 19—21 contain the results of the calculation of the growth for dif-

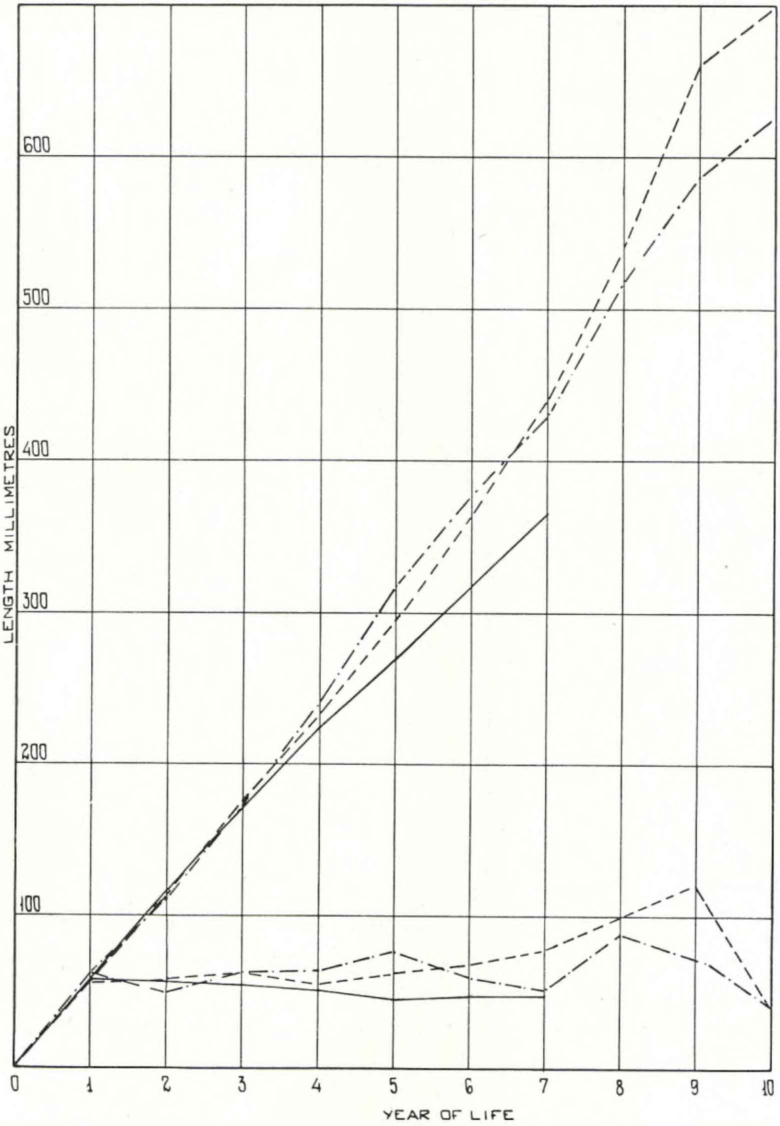

Fig. 9. Calculated general growth and annual increments in length of young trout from the stream ————, spawning trout —·—·—·—, and trout captured in Lake Rensjön — — — —.

ferent year classes of trout caught in the rapids, the pools, and in the fish ladder on its migration to the lake.

Fig. 10 contains diagrams showing the increment in size of the different categories of trout belonging to the same age group and the same year class. These curves show the one-year-old fishes ascending towards the lake to have had a considerably higher increment than the one-year-old individuals of the

Table 20. Calculated growth in length of trout from the pools 1955 (gill-nets).

Year class	Number of fish	Calculated length at the end of year of life 1	2	3	4	5
1953	27	54	119	—	—	—
1952	79	55	109	168	—	—
1951	4	58	120	182	252	—
1950	1	56	129	184	231	283
Average length		56	119	178	242	283
» increment		56	63	59	64	41

same year class (1954) which still stay in the rapids. Among the two-year-old trout of the year class 1953 the ascending fishes show a higher increment than those remaining in the pools, and these in turn exhibit a much better growth than trout of the same age which stays in the rapids. Among the three-year-old trout of year class 1952 the growth is better during the first year of age in the fishes which have been caught in the pools, whereas the ascending trout has strongly increased in size during the later years. Among the four-year-old trout of year class 1951, on the other hand, the fishes which have remained in the pools seem to have during all years of age a certain advance in size as compared with the ascending fishes.

We thus find among the fishes belonging to the same age group those which have had the fastest growth first to begin their ascent towards the lake. This applies first of all to the younger age groups. We find furthermore the trout which stay in the pools with feebler current to have a faster growth than those living in strong currents. This observation militates against the common experience that running water is more productive than sluggish water, and also against statements like that of Schuck and Kingsbury (1945) to the effect that they have found both survival and growth of the hatchery-reared fingerling brown trout in Crystal Creek to be superior in swift running

Table 21. Calculated growth in length of upstream migrating young trout captured in the fish ladder 1955.

Year class	Number of fish	Calculated length at the end of year of life 1	2	3	4	5
1954	4	65	—	—	—	—
1953	37	57	126	—	—	—
1952	63	52	116	176	—	—
1951	14	52	110	176	240	—
1950	4	54	108	172	223	274
Average length		56	115	175	232	274
» increment		56	59	60	57	42

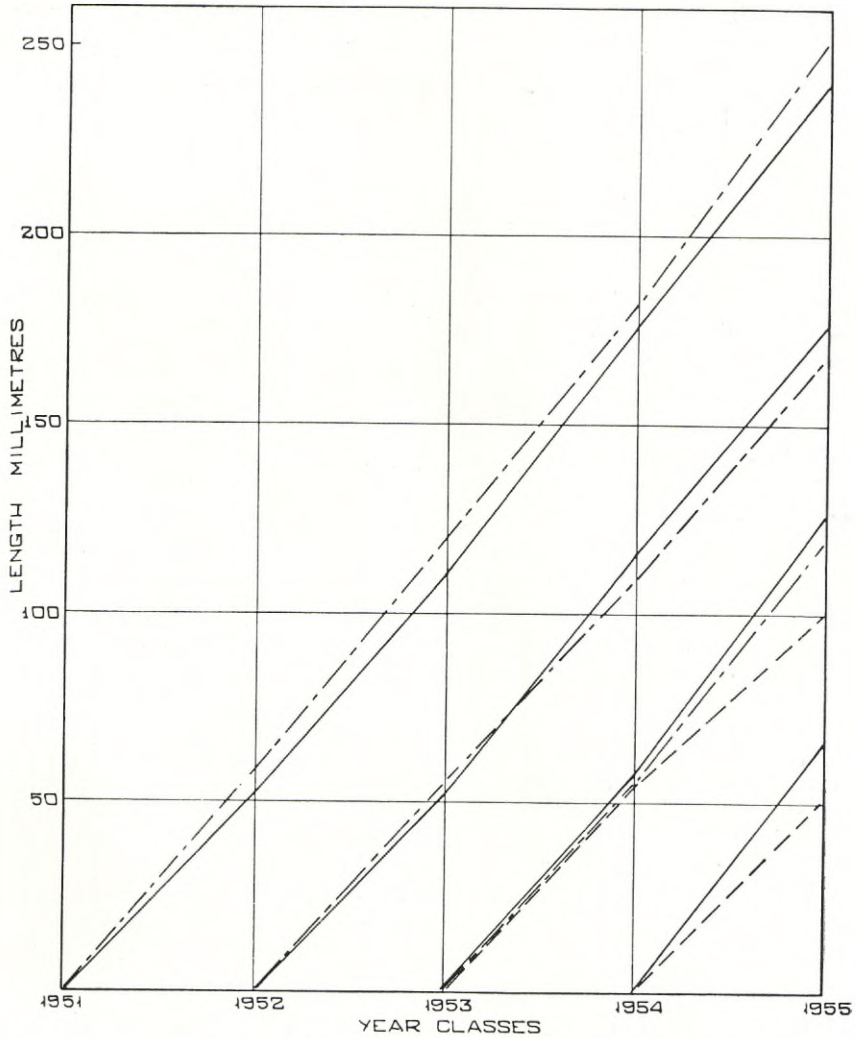

Fig. 10. Calculated growth of the year classes 1951—1954 of trout captured in the fish ladder ————, in the pools —·—·—·—, and in the rapids — — — —.

water than in slow water. According to NILSSON the Rensjö trout living in the pools exhibits a certain tendency of feeding on fish and frogs, though not to the same extent as the trout in the lake. From the point of view of nutrition the pools thus form a transition between swift running water and lake.

The movement of the Rensjö trout from the rapids into the slower water of the pools and, farther up, into the lake brings it gradually under the influence of better nutritional conditions with, consequently, ameliorated growth. HUITFELDT KAAS has also pointed out that the trout seems to exhibit a certain tendency of moving towards more favourable nutritional conditions.

Table 22. Weight (grammes) of trout captured in Lake Rensjön at different age (number of summers).

Number of summer zones									
2	3	4	5	6	7	8	9	10	11
27 (1)	93 (4)	107 (29)	170 (101)	266 (76)	464 (36)	685 (10)	825 (7)	1200 (1)	2738 (4)

If we now return to the general growth of the Rensjö trout caught in the lake (Fig. 9) we find it to be good in this form of trout. At the age of 10 years this trout reaches a length of about 70 cms., and during the first 10 years of life the average annual increment in length is 70 mms. This increment can be compared with that found by HUITFELDT KAAS for the trout populations of the large Norwegian lakes Mjösen and Tyrifjord in which the average annual length increment was 78 and 70 mms., respectively.

The Rensjö trout can also be placed under the same heading as the trout from Kallsjön (RUNNSTRÖM 1951) which likewise shows an annual length increment of 70 mms. It reaches, however, not the same size as the Vättern trout (ALM 1929) with its length increment of 85 mms. A common feature for all these big-sized trout populations is their shifting to a fish diet after the emigration into the lakes.

Table 22 shows the weight of the Rensjö trout at different ages. The figures given are based upon weighings carried out at the capture during summer fishing. For this reason the age is given as the number of summers.

Figure 11 at last contains a representation of the length-weight relation of the Rensjö trout. The mean value of the coefficient of condition for trout between 15 and 40 cms.' length was 1.39.

The Seasonal Growth

Samples of the scales have been taken of the ascending trout in the fish ladder with certain intervals throughout the season of migration (June—September). This material therefore permits certain studies of the season's growth of the Rensjö trout.

Among the scales taken from fishes caught in June specimens are found in which the last-formed annulus is situated near the edge of the scale, whereas others possess a narrow marginal zone of new growth. In Table 23 the percentage of fish with new growth is shown with its distribution over different age-groups and different times of the summer.

During the later half of June all fishes of age-group II have already started to develop a new growth zone. In age group III, on the other hand, only 58 % of the examined individuals exhibit a marginal growth, and in age groups IV

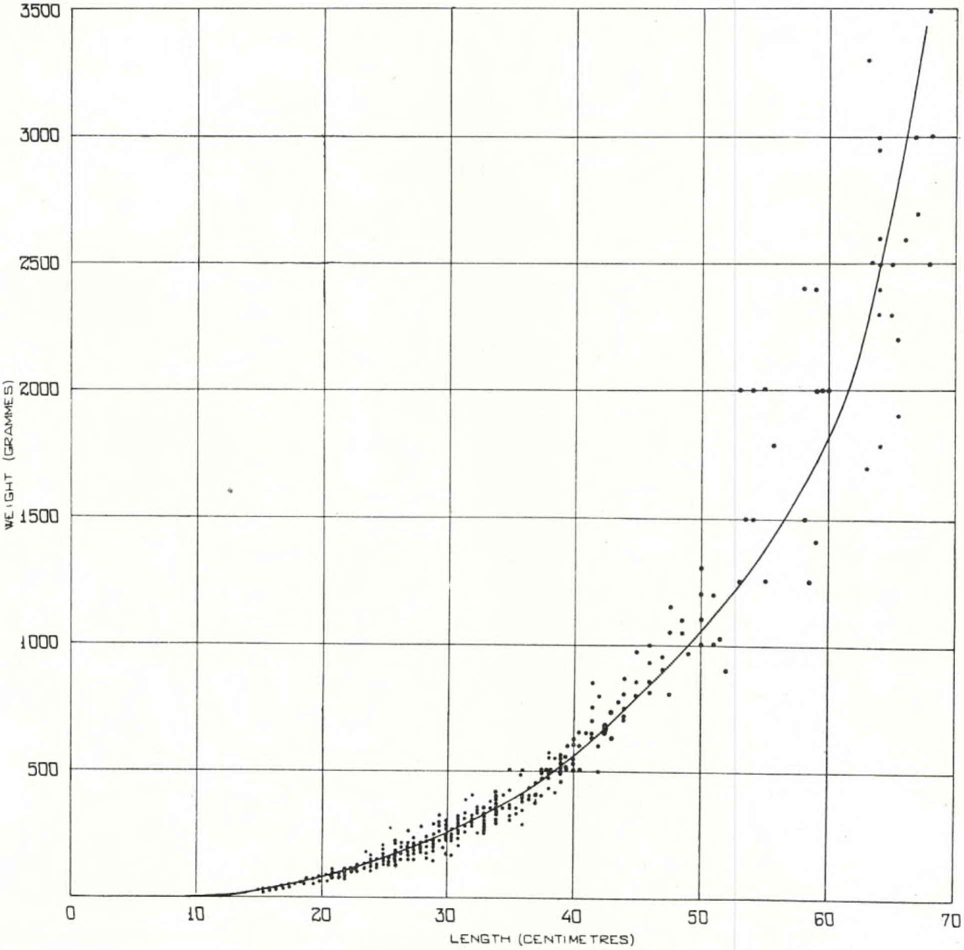

Fig. 11. Length-weight relation of the Rensjö-trout.

and V the figure is as low as 38—40 %. During the first half of July all fish of age-groups I—III have started the summer's growth, while this is the case in only 94 % of age-group IV, and 80 % of age-group V. Only during the later part of July all fish have begun a new growth.

It is also possible to compare the calculated length increment for the part of the growing season which preceded capture with the length increment for the entire season as calculated from samples of the same year-class taken in subsequent calendar years. Table 24 shows what percentage of the season's growth had taken place at the time of capture.

For group 0 the measurements have been carried out directly on fingerlings that had been caught in the river at different times of the summer, whereas for older fish the growth has been determined by scale reading. The trout

Table 23. Percentage of fish with new growth zone.

Age at capture	June 16—30	July 1—15	July 16—31	Aug. 1—31
I	—	100.	100	100
	—	(3)	(10)	(1)
II	100	100	100	100
	(4)	(8)	(30)	(29)
III	58	100	100	100
	(33)	(12)	(32)	(36)
IV	38	94	100	100
	(82)	(34)	(24)	(22)
V	40	80	100	100
	(20)	(20)	(8)	(13)

from June were caught in the later part of this month. The fishes from the remainder of the summer were fairly equally distributed over the different months. For this reason the figures do not indicate the growth as completed at the end of the months of July, August, and September, but rather the conditions as they exist in the middle of the respective months. The figures represent mean values based upon observations during different years.

The Table shows that by the end of June age-group 0 had already completed 43 % of the growth of the year, while the corresponding figure for fish of the age-groups II—V which have begun new growth is 12—20 %. In July the age-groups I—III had attained 54 % of the season's growth, while the age-groups IV—V have come up to 38—40 %. In August group 0 has reached 86 % of the growth of the season which is completely terminated in September. For age-groups II—V the growth is found to be considerably lagging behind that for group 0, and even in September growth is still not terminated in these older fish, but the figure for this month corresponds roughly to the value for the group 0 in August. The growth of the older fish is probably not terminated before the beginning of October.

Fig. 24. Percentage of the seasons growth completed at the time of capture.

Age of capture	June	July	Aug.	Sep.
0	43	—	86	100
	(12)	—	(19)	(7)
I	—	54	—	—
	—	(8)	—	—
II	20	54	77	(72)
	(4)	(38)	(29)	(2)
III	18	54	71	90
	(24)	(44)	(35)	(7)
IV	12	38	76	84
	(81)	(58)	(21)	(2)
V	20	40	56	88
	(9)	(24)	(7)	(31)

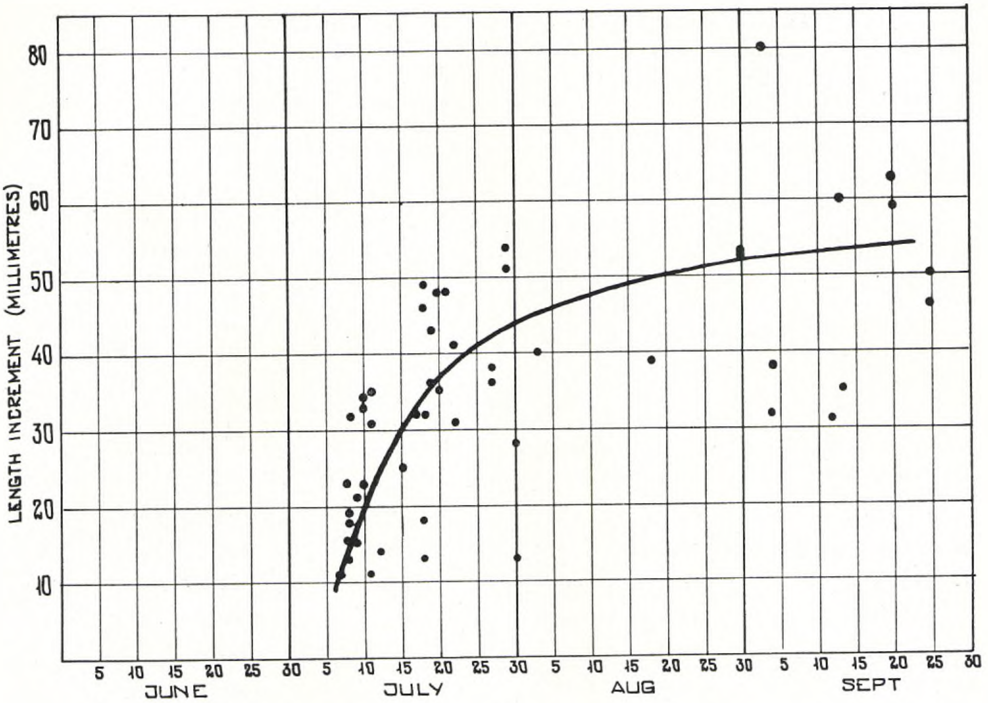

Fig. 12. Seasonal growth of the Rensjö trout in the year 1948.

It thus appears from Tables 23 and 24 that the younger fishes both start and terminate their seasonal growth at earlier dates than the older fishes. This is especially evident in the case of age group 0 in comparison with the older age groups.

While studying the growth of Rock bass from Nebish Lake HILE (1941) has likewise found age to affect the progress of the season's growth. Rock bass of the age-groups V and younger had at capture completed from 11.2 to 28.6 % more of the season's growth than had fish of the age-groups VI and older. He believes the relatively advanced growth of the younger rock bass at capture to depend on an earlier beginning of the season's growth. HILE's observations on rock bass taken on July 1 and 2 in Muskellunge lake indicated that the fish of age groups III, IV, and V had grown sufficiently to exhibit clear-cut annuli at a date when annulus formation was still incomplete in fish of higher age. The present author's observations on the seasonal growth of the Rensjö trout support HILE's conclusions.

For the lake trout (*Christivomer namaycush*) of Great Slave Lake KENNEDY (1954) states that in late June some scales show an annulus at their very edge. In successively later samples more and more scales show annuli. The area outside each new annulus increases until September, when the appear-

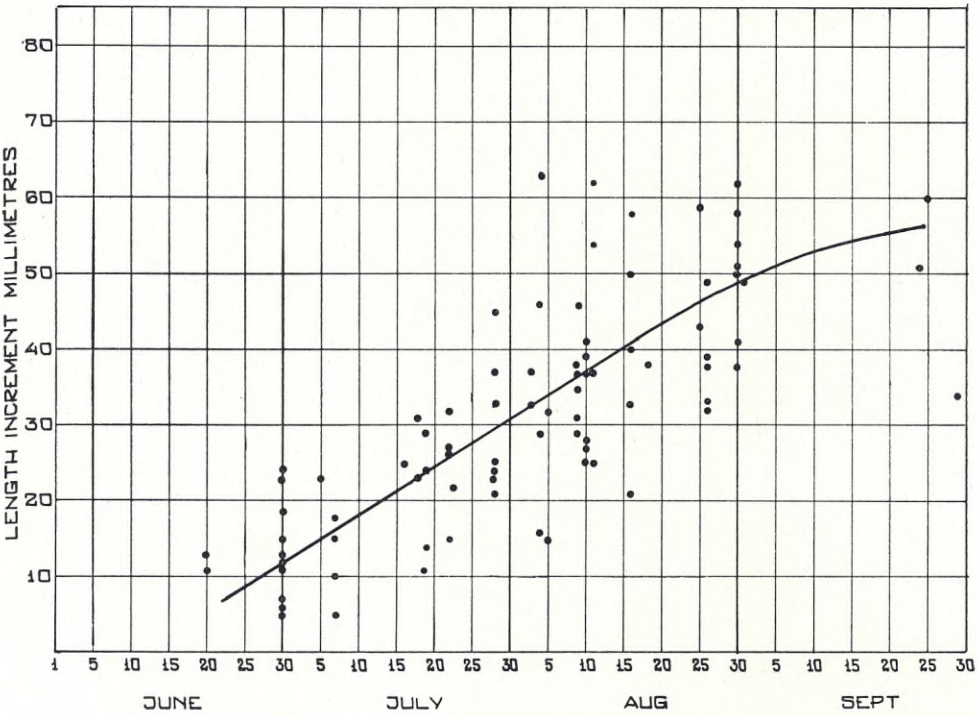

Fig. 13. Seasonal growth of the Rensjö trout in the year 1949.

ance is again much the same as it was in early June. He comes to the conclusion that the Great Slave Lake commercial trout grows only between late May and the middle of September, and that in average fish about half of the growth is completed during July. This corresponds roughly to the seasonal growth in the group 0 of the Rensjö trout, whereas the season of growth occurs somewhat later for the older fish.

It is, however, probable that the seasonal growth varies from year to year on account of the climatic conditions. This becomes obvious from Figs. 12 and 13 which show the seasonal growth of the trout in Rensjöån during the summers of 1948 and 1949.

In 1948 a very vigorous growth took place during July, when the greater part of the seasonal growth was attained. During August and September growth had practically ceased. In the summer of 1949, on the other hand, the trout exhibited a growth which was more uniformly distributed over July and August. At the end of July 1949 the trout had increased in length by only about 30 mms. as against about 45 mms. at the end of July 1948.

In both years the trout had reached about the same length increment by the end of August. The length increment in September seems to have been inconsiderable in either year.

On comparison of the temperature conditions during the two summers (Figs. 16) the year 1948 is characterized by a very high temperature in July, while the mean temperature for August was below normal, and that for September slightly above normal. In 1949 the mean temperatures were low for July and August, while that for September was very high. The high temperature during July 1948 has obviously exerted a strong influence upon the growth, whereas the low temperature of July in 1949 has resulted in a poorer growth. The temperature of September, on the other hand, seems to be of smaller importance for the growth. The high mean temperature of September in 1949 has not brought about any considerable amelioration of the increment of the trout in this month, but the greater part of the season's growth seems to have been completed at the end of August.

Fluctuations in the Strength of Year-classes

As could be seen in Table 12 there occurred in the strength of age-groups among the fish ascending towards the lake certain fluctuations which could in part be explained by the appearance of certain rich year-classes.

The fluctuations in the strength of the year-classes become more evident in a graphical representation of the distribution in per cent of the ascending immature fish (Fig. 14).

It is possible here to distinguish three year-classes which rise above the others, viz. the year-classes 1943, 1947, and 1953 which have been distinguished by different markings.

Table 25 contains a compilation of the number of ascending fishes of the year classes 1942—1953 distributed over the age groups I—V. As can be seen only the year classes 1946, 1947, and 1948 are represented by all age groups, whereas the remaining year classes are incomplete, owing on the fact that the series of observations has not covered a sufficient number of years. A contributing reason lies in the fact that no observations about the upstream migration had been made in 1954. On this account a direct comparison between the numbers of fish represented by the different year class is not possible.

It ought, however, to be possible to apply here the method used by HILE (1941) in his studies of the annual differences in growth rate. A comparison of the strengths of corresponding age groups ought to supply a means of calculating the relative strength of the different year classes. The method is apparent from Table 26. The last column gives the strength of the different year classes with reference to the strength of year class 1942. The 1942—1953 mean of the percentages determined in this manner was, however, +69.4, and the strength of the year class 1942 must have been 69.4 per cent below the 12-year average. The substraction of 69.4 per cent therefore served for the

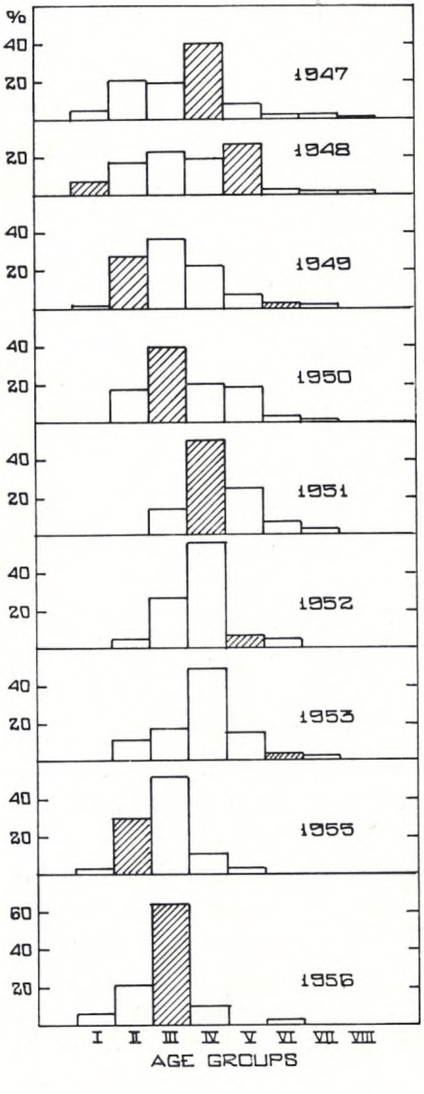

Fig. 14. Average age composition of the upstream migrating young trout in the years 1947—1953 and 1955—1956, expressed by percentage.

conversion of the deviation of each year-class from the 1942 class into a deviation from the 1942—1953 average. These deviations are listed in Table 27. Fig. 15 demonstrates the fluctuations in the relative strength of year-classes 1942 to 1953.

The year 1942 gave rise to a very weak year-class. This was due to the fact that the dam gates were kept closed during the greater part of the summer, and that the flow of water in the river was inconsiderable. It is rather surprising that this year-class has at all contributed to the recruitment of the stock of trout in Rensjön. Of the other year-classes that of 1943 is very strong. This is followed by a decline in 1944. Then follow two moderately strong

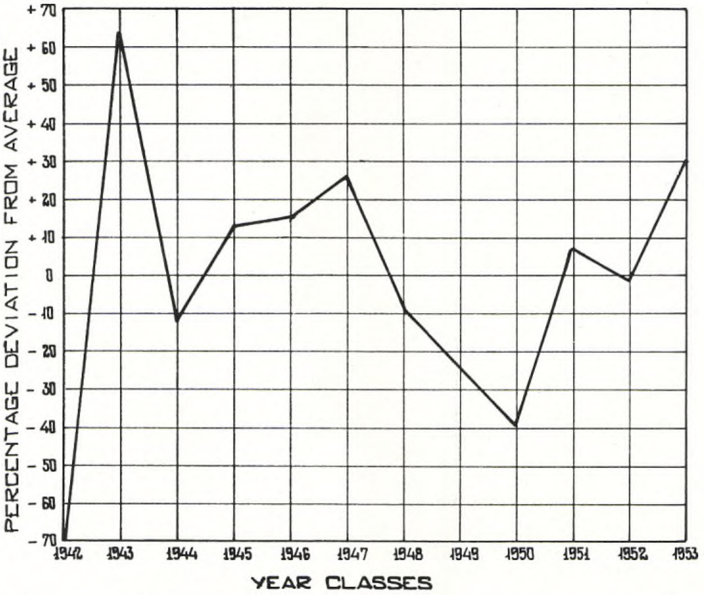

Fig. 15. Fluctuations in the relative strength of the year-classes 1942—1953 of the Rensjö trout.

year-classes in 1945 and 1946, and after them the strong year-class 1947. The two succeeding year-classes, 1948 and 1949, are weak, while 1950 is exceptionally weak. The year-classes 1951 and 1952 are more normal. In 1953 at last a strong year-class is again produced.

Hile (1941) has discussed in detail the correlation between the fluctuations in the strength of the year-classes of the Lebish Lake black bass and the meteorological conditions. He found that high temperatures, especially in the early part of the season, show a decidedly positive correlation with the strength of the year classes. He is of the opinion that high temperature might possible improve food conditions for, and thus promote a more abundant survival of young fish. He found the conditions in June to be more important than those prevailing in other months.

Table 25. The data given in table 12 arranged according to year classes and agegroups.

	Year classes											
Age groups	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953
V	55	269	43	110	112	35	76	?	10	0	—	—
IV	—	263	198	134	119	223	268	246	?	36	33	—
III	—	—	128	233	216	239	64	129	87	?	164	226
II	—	—	—	136	180	163	101	0	24	55	?	96
I	—	—	—	—	29	72	5	0	0	0	0	?

Table 26. Tabulation of data employed in the determination of fluctuations in the abundance of year classes of the Rensjö trout.

Year	Strength in earlier year	Strength in later year	Mean	Change in strength	Percentagd change	Strengt in relation to year class 1942
1942—43	55	269	162	+214	+132.1	+132.1
1943—44	532	241	387	—291	—75.2	+56.9
1944—45	369	477	423	+108	+25.5	+82.4
1945—46	613	627	620	+14	+2.3	+84.7
1946—47	656	732	694	+76	+11.0	+95.7
1947—48	732	514	623	—218	—35.0	+60.7
1948—49	438	375	407	—63	—15.5	+45.2
1949—50	129	111	120	—18	—15.0	+30.2
1950—51	34	55	45	+21	+46.7	+76.9
1951—52	36	33	35	—3	—8.6	+68.3
1952—53	164	226	195	+62	+31.8	+100.1

Table 27. Deviation of the strength of year classes of the Rensjö trout from the average for the year classes 1942—1953.

Year classes											
1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953
—69.4	+62.7	—12.5	+13.0	+15.3	+26.3	—8.7	—24.2	—39.2	+7.5	—1.1	+30.7

In order to test the correlation between the fluctuations of the year classes of the Rensjö trout and the temperature conditions the present author has made use of the temperature of the air observed at the nearest meteorological station, viz. that of Storlien. A comparision between the temperatures of the air at Storlien and the temperature of the water in Rensjöån, which was observed every day during the period 1949—1953, shows very good agreement.

In Fig. 16 a representation has been given of the deviation from the mean air temperature at Storlien during the months June to September from 1942 to 1953. From this it is evident that the only common factor shared by the years 1943, 1947, and 1953, in which strong year-classes were produced, is the high temperature of the month of June. The temperature of this month was above normal also during the years which gave rise to the moderately strong year classes 1945 and 1946.

The very strong development of year-class 1943 can depend on the fact that it was preceded by a couple of feeble year classes, the river being nearly dry during the years 1941 and 1942 as the result of the regulation of Rensjön. Neither is it possible to disregard the fact that the damming up of Rensjön has caused in the lake a flourishing of the plankton which in the form of organic drift has benefited the fry in Rensjöån. NILSSON has shown that the fish of one summer's age in Rensjöån lives mainly on planktonic crustacea

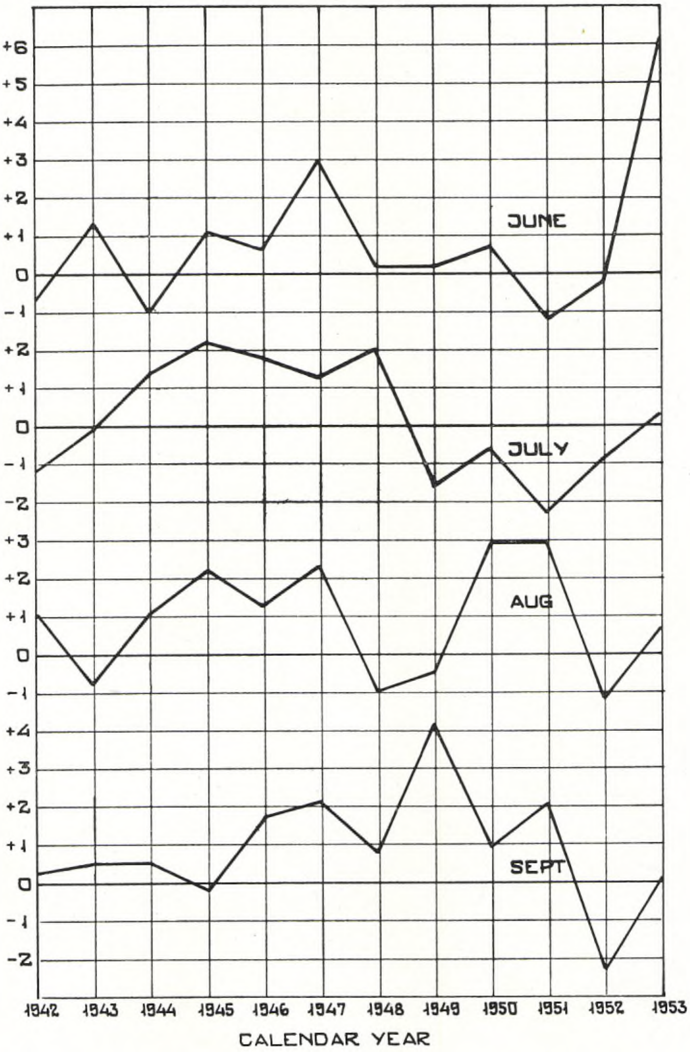

Fig. 16. Deviation from the mean airtemperatures at Storlien for the months June-September during the period 1942—1953.

which are transported from the lake by the current. The year-class 1947 has on the other hand been preceded by two moderately strong year-classes, and that of 1953 by two year-classes of normal and more than normal strength.

HILE writes that the close correlation between the temperature of June and the strength of year-classes suggests the possibility that the relative strength of year-classes of Nebish Lake rock bass is determined by the rate of survival in the very early lives of the individuals. The eggs of Rensjö trout hatch in the first days of May. According to STUART (1953) the hatching of the ova and the feeding of the alevins is separated by an interval of about 29 days, but unfavourable weather conditions can lengthen this time. STUART remarks that retardation of development due to severe weather during the period of the absorption of the yolk sac must be of considerable values to the species, since it ensures the emergence of the alevin from the gravel at a time, when food organisms are available, the activities of the latter being seemingly governed by the same factors of which temperature is presumably the most important. It therefore seems as if the first day in June were those in which the fry of the Rensjö trout is to start their search for food, and we have seen above that June is the month in which for the trout of one summer's age the most vigorous growth takes place.

The similar correlation between the temperature in June and the production of strong year-classes which has been established for two species of fish as different as the Nebish Lake rock bass and the Rensjö trout, living in geographically widely distant regions, must provide a strong support for the assumption that meteorological conditions produce important effects on the strength of the year-classes.

HILE likewise established the simultaneous occurrence of an exceptionally strong year-class 1923 of rock bass in three of four lakes for which data were available.

VAN OOSTEN and HILE (1947) observed the occurrence of the strong year-classes of 1922 and 1926 of the whitefish in Lake Erie, but were unable to establish any correlation with the fluctuations of the meteorological and limnological conditions.

The simultaneous occurrence of strong year classes in 1926 of the autumn-spawning whitefish and of six other spring or early-summer species supports, in the opinion of the authors, the belief that the strength of year classes of whitefish can be determined by conditions at or near the time of hatching in spring.

According to HILE (1954) a preliminary analysis has supplied strong evidence in favour of correlation between certain meteorological conditions and the fluctuations in the strength of the year-classes 1917—1928 of the Saginaw Bay walleye. The indicated relation failed, however, entirely to hold good for year classes of the 1943 collections, and HILE is of the opinion that further inquiry into factors influencing the strength of year-classes of this species must be postponed until a time, when more information, covering a longer series of years, will be available.

Also Le Cren (1955) found similar and synchronous fluctuations in the strength of the year-classes of perch in several lakes of the Windermere region, and suggested that indirect climatic factors working through the food supply of the fry might be of importance.

Observations showing similar fluctuations in the strength of the year-classes in different species of fish are available also from Swedish lakes. Thus

Svärdson (1951) found the whitefish (storsik) of the year-class 1945 in Lake Brunträsk to be unusually numerous, and pointed out that the whitefish population of the river Gimån studied by Toots (1949) had a strong 1945 year-class. The same observation was made by Runnström (1951) concerning the char in Lake Torrön. Svärdson believes this fact to point to a climatic factor as responsible for the change.

The year-class 1947 was very strong not only in the Rensjö trout, but also in the whitefish in the lake Stora Skeppträsket (Svärdson 1951). According to unpublished observations also the year-class 1953 of the grayling in Lake Juveln and of the whitefish in Lake Flåsjön was strong like that of the Rensjö trout.

Thus many indications point towards an influence of the climate upon the strength of the year classes. It is, however, probable that also many other factors play an important rôle. Thus Svärdson (1956) has recently pronounced it as probable that in the case of the Cisco (*Coregonus albula*) in Lake Mälaren strong year-classes reduce the following year classes by cannibalism.

The program of the Institute of Freshwater Research at Drottningholm also comprises extended periodical studies of the fluctuations in age and growth of different species of fish, and every year a vast material is collected from a great number of lakes by test fishing with standard nets. Once the study of this material is further advanced, a more detailed elucidation of the here discussed problem ought to be possible.

Fluctuations in Growth Rate

The data given in Table 18 have formed the basis for the calculation of the annual increments in length for various age-groups of ascending young trout from Rensjön. The results are given in Table 28. Subsequently the deviation of growth in different calendar years from the average for the 11 years' period 1943—1953 has been calculated according to the method of Hile (1941) (Table 29). Since Hile had found that in the rock bass the

Table 28. Annual increments of growth in length of various age groups of upstream migrating trout in the fishladder.

Year of life	Increment of length (mm.) in calender year											
	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953
6	—	—	—	—	—	72	81	47	15	33	43	47
5	—	—	—	—	32	50	61	44	65	42	35	41
4	—	—	—	55	47	52	53	54	54	57	53	34
3	—	—	53	47	49	60	61	53	60	58	59	60
2	—	51	52	49	53	55	67	59	60	64	60	64
1	62	59	58	60	58	66	64	55	60	56	52	54

Table 29. Deviation of growth of the trout in different calendar years from the average for the 11 year period 1943—1953.

	Percentage deviation from average growth in calendar year										
	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953
Growth in the first year ...	+1.3	—0.4	+3.0	—0.4	+12.5	+9.4	—5.7	+3.0	—3.9	—11.3	—7.5
Growth in the second and later years	+0.2	+2.1	—6.9	—8.2	+9.9	+21.0	—1.7	—2.9	—2.9	—4.5	—6.1

growth in the first and in the second and following years fluctuated in a different manner, these two groups have been kept apart in our Table. In Fig. 17 are shown the fluctuations in growth during different calendar years for fish of one year's age as well as for older fish.

Hile found the growth of older individuals of the Lebish rock bass to be more closely correlated with the temperature in June and September than with the conditions during other months. The growth during the first year, however, did not seem to be correlated with either temperature or precipitation. In the case of the Rensjö trout we have found the most vigorous growth of the one-year-old fish to take place during June and July, and that of the older trout during July and August, while the temperature conditions during September exert little influence upon the growth. It is therefore to be expected that the growth of the trout of one summer's age will show a correlation with the temperature in June and July, that of the older fish with the temperature in July and August, and that the growth of the two groups will fluctuate in different ways.

With regard to the fluctuations in growth-rate during the first year of life we find a very good growth in 1947 and 1948, a growth slightly higher than normal in 1945 and 1950, a normal growth in 1943, 1944, and 1946, and a poor growth in the years 1949, 1951, 1952, and 1953.

It can be established immediately that no correlation occurs during the first year of life between strong year classes and fast growth. Growth was good during the first year of life only for the year-class 1947, whereas it was normal for year-class 1943, and poor for year-class 1953. For this reason the temperature in June can not have been the only deciding factor for the growth. In 1947 the high temperature in June was followed by a fairly high temperature in July, whereas in 1943 and 1953 the temperature of July was normal. In the case of other years, in which the growth during the first year was above average, we find for 1948 a temperature in June which was somewhat above the mean temperature, and a very high temperature in July, and for 1945 a higher than normal temperature in June and a very high temperature in July. In 1950 the temperature was higher than normal in June, but below normal in July. During the years with poor growth, viz. 1949, 1951,

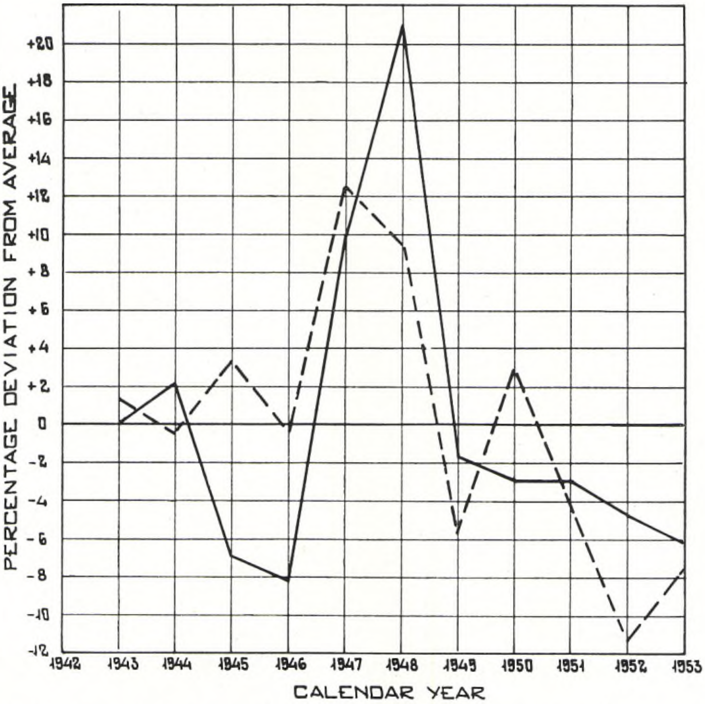

Fig. 17. Fluctuations in growth in the calendar years 1942—1953 of one year old trout ——— and older trout — — — —.

and 1952, the temperature of June was normal or lower, whereas the temperature of July was low in all these years.

A certain correlation can thus be found between the growth of the Rensjö trout during its first year and the temperatures of June and July, but deviations do occur. Particularly remarkable is the poor growth of the year 1953, when the temperature was unusually high in June, and slightly above normal in July.

An examination of the fluctuations in the growth of the older fish shows a very fast growth in 1947 and 1948, and a slightly more than normal growth in 1944, whereas the growth in the other years falls below the average. Here it is difficult to discover any correlation between the growth and the temperature conditions during the period of growth. The warm months July and August in 1947 might explain the vigorous growth in this year. The same temperature conditions reigned, however, also in the years 1945 and 1946, when the growth of the trout was very poor. In 1948, when the growth of the trout was best, July was admittedly warm, but the temperature of August was below normal. It can also be observed that the high temperature of the month of August in 1950 and 1951 was not able to make up for the low temperature of July as far as growth is concerned.

The relation between temperature and growth in the older Rensjö trout is thus not in agreement with HILE's experience with rock bass from both Nebish Lake and Muskellunge Lake, where this author found a strong positive correlation between the annual fluctuations of temperature and the growth rate.

We must, however, not overlook the possibility that other factors might prevail over the influence of the meteorological conditions, and HILE, e.g., points out that fluctuations in the strength of year-classes may be reflected in the growth rate in later years.

Among the trout which is a decidedly territorial fish there must exist a strong individual competition. The production of a numerous year-class must therefore cause a slow growth during the immediately following years. The abundance of trout that must have existed for some years following the production of the extremely strong year class of 1943 may well have contributed to the slow growth during the years 1945 and 1946. In the years 1947 and 1948 the major part of year class 1943 had ascended into the lake. In the same way the strong year class 1947 can have held back growth during 1949 and the immediately following years. It is, however, hardly possible to explain the slow growth during 1953 by the abundance of fish, since at that time almost all individuals of the year-class 1947 had ascended into the lake. Neither does the slow growth of the Rensjö trout in 1953 agree with the conditions observed in other lakes. Thus the whitefish from Lake Skeppträsk exhibited in this year a fast growth (SVÄRDSON 1957). According to unpublished observations also the whitefish in Lake Flåsjön showed good growth in this year, and the same applies to the year-class 1953 of the grayling in Lake Juveln. In 1953 there must have existed in Rensjöån certain local conditions which contributed to the slow growth of the trout in this year.

The fact that the growth during the year immediately after the production of a strong year class, like 1944 and 1948, does not exhibit a strong decline might depend on the circumstance that the members of the strong year-classes frequent during their second summer another habitat than the older fish.

It has been pointed out already earlier that the Rensjö trout of age group I stays mainly in the rapids, whereas the older fish stays in the pools (cf. Fig. 6).

Also group 0 of the Rensjö trout stays in the rapids, but in their very shallow parts with slower current, where it is not exposed to competition on the part of the older fish. NILSSON (1957) has also shown that trout of the group 0 lives mainly on food which differs from that of the older fish. It is thus explainable that during the first year the growth of the Rensjö trout shows a closer correlation with the temperature conditions than what is the case for the older trout which is influenced in a higher degree by the abundance of fish.

Summary

1. The level of Lake Rensjön is regulated by a dam across the outlet of the lake into Övre Rensjöån. A fish ladder in the dam permits the passage of the fish. Observations about the migrations of the fish in the ladder have been carried out during 1947—1953 and 1955—1956. During some years also the migration in the lower course of Rensjöån has been checked by means of fences erected at the mouth of the river into Lill Korsvattnet and Korsvattnet. Test fishing has been carried out in Rensjön and in different parts of Rensjöån.

2. In Rensjön brown trout, char, and burbot are found. The trout descends into Rensjön for spawning, and the fish growing up in the river ascends into the lake. During the entire time of observation the counting in the ladder gave 138 descending spawning trout, 131 spent trout, and 4952 ascending young trout. The ladder was in addition passed by 699 char on its way up to the lake.

3. The ascending young trout is made up mainly of the age-groups I—V among which dominate age-groups II and III. In the river the younger age-groups stay preponderantly in the rapids, and the older age-groups in the pools with their quieter water. The descending spawning fish is composed of age-groups IV—XII.

4. The spawning trout descends mainly in August and September, and ascends into the lake in the course of the following spring and early summer. Experiments with the marking of fish seem to show that not all descending fish return into Rensjön, but that part of them remains farther down-stream in the watercourse. This is compensated to a certain extent by the ascent of spent trout from the lakes lower down. The majority of the Rensjö trout spawns only every other year.

5. The ascent of the young trout commences after the breaking-up of the ice upon the lake and after the rise of the temperature of the water. This usually takes place at the beginning of June. The termination of the migrations falls as a rule into the beginning of October, when the temperature of the water drops considerably. Quick rises in temperature stimulate the migration, presumably by increasing the activity of the fish. Marking experiments show the ascending young fish to be recruited from the stock of trout in Lill Rensjön, while few trout continue further up-stream into Stor Rensjön. The stock in this lake is derived mainly from the feeding brooks. Altogether 14.8 per cent of the marked trout have been recaptured. On the basis of the marking experiments the stock of trout in Lill Rensjön (area 297 hectares=734 acres) has been calculated to 1100—1300 fish.

6. The ascending char consists mainly of adult maturing fishes which must be derived from the lakes farther down-stream. In opposition to the trout

most of it ascends into Stor Rensjön, where a great part of the fish has been recaptured in the same autumn upon the usual spawning grounds of the char.

7. On the basis of the age composition of the Rensjö trout the survival after the ascent into the lake has been calculated to 72 per cent from age IV to V, 44 per cent from age V to VI, 29 per cent from age VI to VII, and 18 per cent from age VII to VIII. On the basis of the yearly recruitment from the river during the years 1947—1953 and of the calculated survival of the different age-groups the stock of trout in Lill Rensjön in 1953 has been calculated to about 1100 fish. This agrees well with the value obtained on the basis of the marking experiments.

8. The Rensjö trout exhibits a strong increase in growth after the ascent into the lake. This can be linked with its change to a diet of fish. Among the trout upon the river stage the fish which dwell in the pools grow faster than those living in the rapids. This can depend upon the fact that the trout in the pools already exhibit a tendency towards feeding on fish and frogs. The growth of the Rensjö trout is comparable to that of the trout in the great Norwegian lakes Mjösen and Tyrifjord, but remains somewhat behind that of the Vättern trout. A common feature for these stocks of big-sized trout is that they feed on fish after their migration into the lake.

9. With regard to the seasonal growth it can be remarked that a new growth zone is begun upon the scales at the end of June and the first half of July. In the younger age-groups growth starts earlier than in the older. In age-group 0 43 per cent of the growth of the year are completed already by the end of June, and 86 per cent in August. On account of different climatic conditions the seasonal growth varies, however, from year to year.

10. The fluctuations in the strength of the year-classes and their connection with climatic factors, especially the temperature, are discussed. In the Rensjö trout the year-classes 1943, 1947, and 1953 are particularly strong, and these years have in common a high temperature in June.

11. In the trout of one year's age the fluctuations in the growth rate exhibit a certain correlation with the temperature conditions during June and July, while no such correlation between growth rate and temperature can be proved for older age-groups, depending probably upon the circumstance that the fluctuations in the strength of the year-classes may be reflected in the growth rate in later years.

References

ALLEN, K. R. 1951. The Horokiwi stream. *New Zealand Marine Dept. Fish. Bull. 10: 1—231.*

ALM, G. 1929. Undersökningar över laxöringen i Vättern och övre Motala ström. *Medd. Kgl. Lantbruksstyrelsen 276: 1—68.*

— 1950. The sea-trout population in the Åva stream. *Rept. Inst. Freshwater Research, Drottningholm 31: 26—56.*

ARWIDSON, G. 1935. Märkning av laxöring i Vättern. *Rept. Inst. Freshwater Research, Drottningholm 4: 1—16.*

BROWN, M. E. 1946. The growth of brown trout. *Journ. Exp. Biol. 22: 118—155.*

DAHL, K. 1910. Alder og vekst hos laks og örret. Kristiania.

ELSON, P. E. 1942. Effect of temperature on activity of *Salvelinus fontinalis. Journ. Fish. Res. Bd. Canada V: 461—470.*

FABRICIUS, E. 1950. Heterogeneous stimulus summation in the release of spawning activities in fish. *Rept. Inst. Freshwater Research, Drottningholm 31: 57—99.*

GUSTAFSON, K.-J. 1951. Movements and age of trout, *Salmo trutta* LINNÉ, in Lake Storsjön. *Rept. Inst. Freshwater Research, Drottningholm 32: 50—58.*

HILE, R. 1941. Age and growth of the rock bass, *Ambloplites rupestris* (RAFINESQUE) in Nebish Lake, Wisconsin. *Trans. Wisconsin Acad. Sci. Arts and Lett. 33: 189—337.*

— 1954. Fluctuations in growth and year-class strength of the walleye in Saginaw bay. *U.S. Fish and Wildlife Service, Fish. Bull. 91, vol. 56: 1—59.*

HUITFELDT-KAAS, H. 1927. Studier over aldersforholde og veksttyper hos norske ferskvannsfisker. Oslo.

JACKSON, C. H. N. 1939. The analysis of an animal population. *Journ. Animal Ecol.* 8: 238—246.

KENNEDY, W. A. 1954. Growth, maturity and mortality in the relatively unexploited lake trout, *Christivomer namaycush,* of Great Slave Lake. *Journ. Fish. Res. Bd. Canada 11: 827—852.*

LE CREN, E. D. 1955. Year to year variation in the year-class strength of Perca fluviatilis. *Int. Ass. Theoret. and Appl. Limnology. Proceedings XII: 187—192.*

MOTTLEY, C. MC C. 1938. Fluctuations in the intensity of the spawners runs of rainbow trout at Paul Lake. *Journ. Fish. Res. Bd. Canada 4: 69—87.*

NEEDHAM, P. R., J. W. MOFFET, and D. W. SLATER. 1945. Fluctuations in wild brown trout population in Convict Creek, California. *Journ. Wildl. Mgt. 9: 9—25.*

NILSSON, N. A. 1957. On the feeding habits of trout in a north Swedish stream. *Rept. Inst. Freshwater Research, Drottningholm 38: 154—166.*

RUNNSTRÖM, S. 1949. Control of trout migration by a fish ladder. *Rept. Inst. Freshwater Research, Drottningholm 29: 85—88.*

— 1951. The population of char, *Salmo alpinus,* LINNÉ, in a regulated lake. *Rept. Inst. Freshwater Research, Drottningholm 32: 66—78.*

— 1952. The population of trout, *Salmo trutta,* LINNÉ, in regulated lakes. *Rept. Inst. Freshwater Research, Drottningholm 33: 179—198.*

RUPP, R. S. 1955. Studies on the eastern brook trout population and fishery in Sunkhaze stream, Main. *Journ. Wildl. Mgt. 19: 336—345.*

SCHUCK, H. A. 1943. Survival, population density, growth and movement of the wild brown trout in Crystal Creek. *Trans. Amer. Fish. Soc. 73: 209—230.*

SCHUCK, H. A. and O. R. KINGSBURY. 1945. Survival and growth of fingerling brown trout (*Salmo fario*) reared in different hatchery conditions and planted in fast and slow water. *Journ. Amer. Fish. Soc. 75: 147—156.*

SHETTER, D. S. and J. W. LEONARD. 1942. A population study of a limited area in a Michigan trout Stream. *Journ. Amer. Fish. Soc. 72: 35—51.*

SIVERTSEN, E. 1952. Analyser av örretens og rörens vekst i fiskevann i Sör-Tröndelag. *Trondheims Jæger- og Fiskeforening 75 års beretning: 1—32.*

STUART, T. A. 1953. Spawning migration, reproduction and young stages of lock trout (*Salmo trutta,* L.). *Sc. Invest. Freshwat. Fish. Scot. 5: 1—39.*

SVÄRDSON, G. 1951. The coregonid problem. III. Whitefish from the Baltic successfully introduced into fresh waters in north of Sweden. *Rept. Inst. Freshwater Research, Drottningholm 32: 79—125.*

SVÄRDSON, G. 1956. Lambarfjärdens siklöja. *Svensk Fiskeritidskrift 65: 73—80.*

— 1957. Skeppsträsklöjan. *Svensk Fiskeritidskrift 66: 37—42.*

TOOTS, H. 1949. Maränenfischerei im Fluss Gimån (Jämtland). *Rept. Inst. Freshwater Research, Drottningholm 29: 146—152.*

VAN OOSTEN, J. and R. HILE. 1947. Age and growth of the lake whitefish *Coregonus clupeiformis* (MITCHELL), in Lake Erie. *Trans. Amer. Fish. Soc. 77: 178—249.*

Achlya prolifera als Abwasserpilz in einem mittelschwedischen Wasserlauf

Von Ingeborg Stjerna-Pooth

Das Auftreten von sogenannten Abwasserpilzen ist ebensolange bekannt wie die moderne Entwicklung auf dem Gebiete der Industrie und der Wohnhygiene. Der schmutziggraue oder gelbweisse, schlammige Belag des Bodens oder der Ufervegetation in einem Wasserlauf, der von nicht- oder unvollständig gereinigtem Abwasser kommunalen oder industriellen Ursprungs berührt wird, das eine grosse Menge von in Zerfall befindlichen organischen Bestandteilen enthält, ist eine so gewöhnliche und in die Augen fallende Erscheinung geworden, dass die meisten Menschen nun die Bedeutung des Wasserproblems für das moderne Gemeinwesen zu verstehen beginnen. Wenn sie in ihrem früher klaren und reinen See nicht länger waschen, baden oder fischen oder Krebse in ihrem Bach fangen können, weil diese da nicht länger vorkommen, sondern durch den Gestank des Wassers oder den glatten Belag von Abwasserpilzen auf den Steinen fortgejagt werden, denken sie wohl zunächst nicht daran, dass der Pilz primär ihr Bundesgenosse ist, der tut, was er kann, um das Wasser zu reinigen, d.h. von den verunreinigenden Bestandteilen zu befreien. Die Pilze führen, wie bekannt, eine saprophytische Lebensweise, indem sie die Fähigkeit haben, organische Nahrung aufzunehmen und aus deren Verwandlung in einfache unorganische Bestandteile ihren Energiebedarf zu decken. Dass der Pilz in einem an organischen Bestandteilen reichen Wasser eine enorme Entwicklung nimmt und seinerseits zu neuen Unannehmlichkeiten z. Bsp. zu einem beschwerlichen Treiben losgelöster Flocken oder einem unbehaglichen Geruch bei ihrer Verwesung Anlass geben kann, ist mehr eine sekundäre Verunreinigung, die nur allzuoft den Verunreinigungsgrad des Wassers noch vermehrt. Auch aus ästhetischen Gesichtspunkten ist dieses Massenauftreten des Abwasserpilzes eine Plage für die Anwohner und ein Problem des Naturschutzes.

Bisher war nur eine geringe Zahl von Arten bekannt, die durch ihr Massenauftreten in verunreinigtem Wasser als wirkliche Saprobieindikatoren bezeichnet werden konnten. Die gewöhnlichste und bekannteste von diesen Arten ist zweifelsohne *Sphaerotilus natans,* der eigentlich kein Pilz, sondern eine in Fadenform angeordnete Serie von stabförmigen Bakterien ist, die in einer gemeinsamen Scheide eingeschlossen sind. Diese Fäden treten, zusammengeführt zu Zotten oder Klumpen, in oft grosser Menge in den sogenannten polysaproben oder α-mesosaproben Zonen der verunreinigten Gewässer auf, d.h. in den Zonen in denen die eigentliche Zerzetzung der organischen Stoffe, charakterisiert durch Reduktions- und

Spaltungsprozesse, geschieht. Neben dem *Sphaerotilus* findet man, und zwar hauptsächlich in der mesosaproben Zone, sehr häufig einen richtigen Pilz, den zu den Phykomyceten gehörenden *Leptomitus lacteus.* Beide kommen oft in grosser Zahl unterhalb von Siedlungen, Meiereien, Zucker- und Papierfabriken und anderen Anlagen vor, deren Abwässer gelöste organische Bestandteile in grösserer Menge enthalten. Auch einige Arten der gewöhnlichen Schimmelpilze, *Mucor racemosus* und *Mucor zygorrhynchus* sowie eine *Penicillium*art, sollen unter ähnlichen Verhältnissen auftreten können. Schliesslich kennt man als Abwasserpilz den zu den Ascomyceten gehörenden *Fusarium aqueductum,* der besonders in solchen Gewässern auftritt, die von mehr sauren Abwässern z.Bsp. Sulfitlauge, berührt werden. Nur diese fünf bis sechs Arten sowie eine weitere Sphaerotilusart werden in den beiden meist gebrauchten deutschen Handbüchern der letzten Jahre, die das Thema der Abwasserbiologie berühren — KOLKWITZ: Oekologie der Saprobien 1950 und LIEBMANN: Handbuch der Frischwasser- und Abwasserbiologie 1951 — genannt. Da ich den Pilz, der hier behandelt werden soll, die *Achlya prolifera,* in der Literatur in seinem Auftreten als Abwasserpilz noch nicht beschrieben gefunden habe, schien es mir angebracht, eine kürzere Beschreibung seiner Morphologie und seines Auftretens in dem unten angeführten Wasserlauf Hedströmmen unter Hinzufügen einiger historischen Daten zu geben.

Im Anfang des Monats November 1956 erhielt ich in einer Aufwuchsprobe aus dem Fluss Hedströmmen, Västmanland, die unterhalb der im Besitz der A.G. Statens Skogsindustrier befindlichen Holzfiberplatten (Wallboard)-fabrik in Skinnskatteberg genommen war, einige Klumpen und Zotten von typischem Abwasserpilzcharakter. Makroskopisch schien es sich um einen *Leptomitus lacteus* zu handeln, den man bereits früher in diesem Wasserlauf gefunden hatte. Die mikroskopische Untersuchung zeigte indessen, dass es sich weder um *Leptomitus* noch um eine andere der oben genannten Pilzarten handelte. Das Aussehen der Hyfen deutete auf eine Art der Familie *Saprolegniaceae* unter den Phycomyceten hin, und, nachdem allmählich Sporangien und sexuelle Vermehrungsorgane beobachtet und eingehend studiert werden konnten, zeigte es sich, dass es sich um eine *Achlya*art, genauer, um die *Achlya prolifera* DE BARY handelte. Eine Woche später hatte ich Gelegenheit, erneute Proben von dem Pilz an verschiedenen Stellen des Hedströmmen zu nehmen und an Ort und Stelle dessen Vorkommen und Aussehen im Wasserlauf zu studieren. Auf der beigefügten Kartenskizze über den Hedströmmen, Abb. 1, habe ich auf der infragekommenden Strecke zwischen den Seen Övre und Nedre Vettern mit den Ziffern 1—4 die Stellen der zweiten Probeentnahme vom 12 November bezeichnet. Bei der ersten Probeentnahme am 1 November wurden Proben an den Punkten 2 und 4 genommen. Bei Punkt A der Karte befindet sich die Mündung der Abwasserleitung der Fabrik, wo das Abwasser in den Strom gelassen wird, nachdem es ein Schlammbecken für die Absetzung suspendiertes Fibermaterials passiert hat.

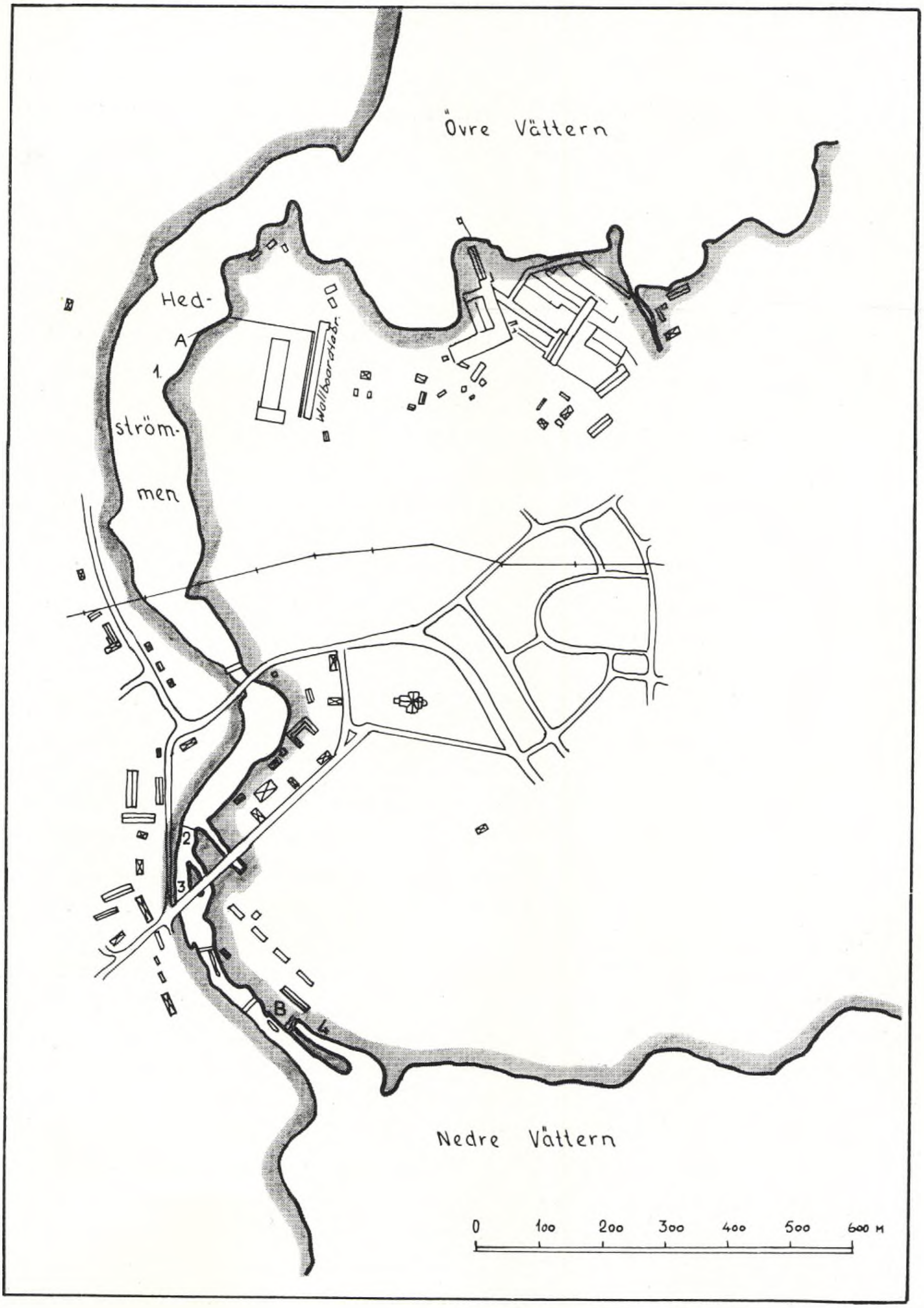

Abb. 1. Karte über den Fluss Hedströmmen zwischen den Seen Övre und Nedre Vettern.

Schon bei Punkt 1, c:a 100 m unterhalb des Auslaufes, kam der Pilz als Aufwuchs auf Zweigen und anderen Gegenständen im Wasser, auf denen er sich festhalten konnte, reichlich vor. Er tritt ganz wie die übrigen bekannten Abwasserpilze auf und, wenn man ihn im Fluss sieht, kann man glauben, es handele sich um *Sphaerotilus* oder *Leptomitus*. Etwas weiter unterhalb, in dem in diesem Teil erweiterten Flussbett, wird er noch üppiger und bildet da eine zusammenhängende graugelbe Masse auf den Steinen, die von den Brücken der Landstrasse und der Eisenbahn, c:a 600 m unterhalb des Auslaufes, gut wahrnehmbar ist. Die Stromstrecke oberhalb Punkt 2 auf der Karte ist für das Kraftwerk des Ortes, das bei Punkt B gelegen ist, reguliert. Eine Rohrleitung führt das Wasser des Flusses von einem Punkt unmittelbar oberhalb Punkt 2, wo zwei Deichtore eine Sperre gegen den unteren Teil des Hedströmmen bilden, zum Kraftwerk. Das Flussbett ist in diesem unteren Teil bedeutend enger, und die Wasserführung im allgemeinen sehr gering. Die Steine des Bodens liegen teilweise über der Wasseroberfläche. Der Pilz, der bei der zweiten Probeentnahme bei Punkt 2 als Aufwuchs auf einem Bretterboden, über den das Wasser in einem dünnen Strom durch die Deichtore lief, sowie auf Punkt 3 als schlüpfrige dunkle Klumpen und helle Zotten in geringerer Menge auf den Bodensteinen gefunden wurde, war hauptsächlich *Leptomitus*. Punkt 4 schliesslich liegt unmittelbar unterhalb des Kraftwerkes in einer gut 100 m langen kanalähnlichen Bucht des Sees Nedre Vettern, der sich parallel zum Auslauf des Hedströmmen in den See erstreckt. Die teilweise mit Steinplatten belegten Uferseiten des Kanals waren dicht besetzt mit kräftigen Flocken der hier ganz dominierenden *Achlya prolifera*. Selbst ein Teil des Seeufers war mit dem Pilz bewachsen, der einen Überzug auf allen Gegenständen bildete, die sich unter der Wasseroberfläche befanden. Die *Achlya* trat also hauptsächlich in dem Teil des Wasserlaufes auf, der die grösste Wassermenge und die stärkste Strömungsgeschwindigkeit aufwies. Bei der ersten Probeentnahme fand sich eine geringere Menge dieses Pilzes auch bei Punkt 2 und zwar hauptsächlich im Stadium der sexuellen Vermehrung. Da aber dieses in der Entwicklung des Pilzes spätere Stadium oft auf weniger geeignete Milieuverhältnisse, z.Bsp. geringeren Nahrungszugang hindeutet, ergibt sich, dass er in diesem mehr oder minder trockengelegten Teil des Flussbettes nicht richtig gedeiht.

Der Name *Achlya prolifera* taucht in der Literatur schon im Jahre 1760 auf, wo die Art als eine Alge, verwandt mit *Conferva* und parasitierend auf Fliegen, genannt wird. Mehrere Forscher bezeichneten sie im Anfang des neunzehnten Jahrhunderts einmal als Alge, ein anderes Mal als Pilz, auf Tieren im Wasser vegetierend, so der Schwede ARESCHOUG, der im Jahre 1845 in einem Brief an LOVÉN mitteilt, dass er die *Achlya prolifera* als Parasit auf *Leuciscus idus* im Wallgraben von Göteborg gefunden habe. Als Synonyme zu dieser Pflanze nennt ARESCHOUG *Vaucheria aquatica, Lyngbya* und *Leptomitus clavatus* AGARDH. Alle diese Forscher waren indessen auf einer falschen

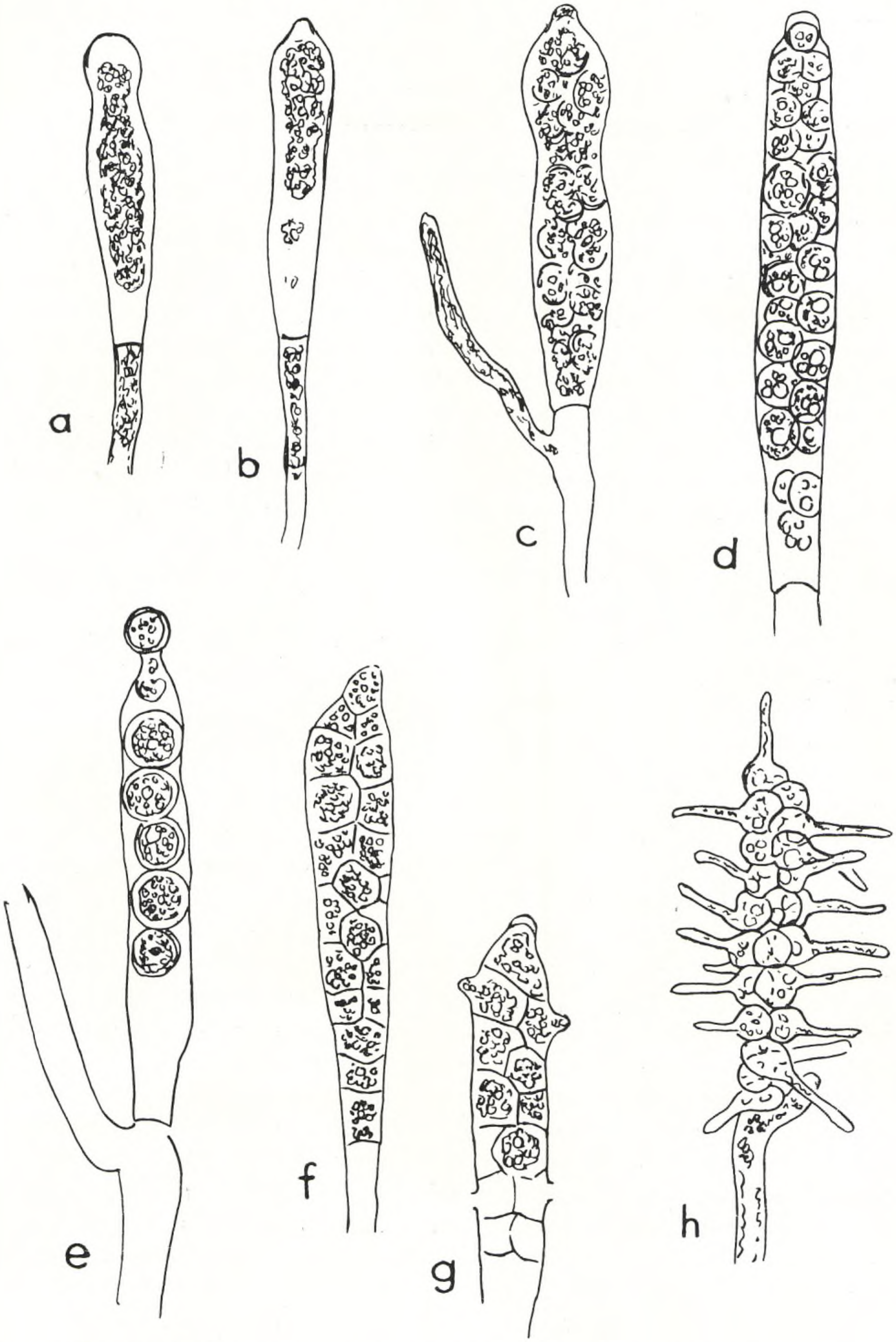

Abb. 2. Die Sporangien- und Sporenbildung: a—d. Normaler Verlauf. e. Einige Sporen bleiben im Sporangium und häuten sich da. f—g. Netzsporangien. h. Sporen von Aplanestypus.

Spur, da deren *Achlya prolifera* überhaupt keine *Achlya-,* sondern eine *Saprolegnia*art nämlich *Saprolegnia ferox* war, was endgültig von DE BARY 1852 festgestellt wurde. In seiner in diesem Jahr veröffentlichten eingehenden Beschreibung der wirklichen *Achlya prolifera,* die die vegetativen und sporangientragenden Stadien umfasste, nennt DE BARY CARUS (1823) als den ersten, der diesen Pilz als eine *Achlya* beschrieben und abgebildet hat. Auch DE BARY fand seine *Achlya prolifera* auf toten Insekten in einem Torfstich im Grunewald bei Berlin im November 1851. Später folgten mehrere Abhandlungen von DE BARY, in denen er auch den Verlauf der sexuellen Fortpflanzung sehr eingehend beschreibt und abbildet. Mit seiner Arbeit muss die Morphologie und der Verlauf der Entwicklung des Pilzes als vollständig bekannt angesehen werden. Was später in Handbüchern und Floren gesagt wird, stützt sich ganz auf die Beschreibung von DE BARY.

Über die Verbreitung der Art äussert sich DE BARY 1888 in der Weise, dass er sie »die häufigste aller *Achlya*arten, die wohl überall sich finden dürfte« nennt. In dieser Hinsicht dürfte er sich indessen geirrt haben. In den U.S.A. scheint die Art nach COKER (1923) und COKER and MATTHEWS (1937) überhaupt nicht gefunden worden zu sein, und die Funde in Europa waren offenbar nach DE BARYs Zeit selten. In Dänemark, wo zuerst PEDERSEN (1909) und später LUND (1934) eingehende Untersuchungen über dänische Phykomyceten angestellt haben, ist sie ebenfalls nicht gefunden worden. Unter den elf Arten, die LUND in seiner Zusammenstellung der in Dänemark gefundenen *Achlya*arten, die an einer grossen Anzahl Stellen gesammelt waren, aufführt, bezeichnet er die *Achlya racemosa* als die gewöhnlichste. In Lettland hat *Apinis* (1930) Untersuchungen über die Saprolegniacéen betrieben. Auch er nennt die *Achlya prolifera* unter den von ihm gefundenen Arten nicht. Von den nordischen Ländern ist merkwürdigerweise ein Fund von *Achlya prolifera* nur aus Schweden, wo man überhaupt keine Untersuchungen dieser Pilzgruppe vorgenommen hat, bekannt geworden. Der Schweizer GÄUMANN (1918) fand bei einem Besuch in Abisko eine Anzahl Saprolegniacéen im Torne träsk, unter ihnen zwei *Achlya*arten: *Achlya racemosa* und *Achlya prolifera.* Der Fund der letzteren wird nur ganz kurz ohne irgendwelche Beschreibung des Pilzes erwähnt.

Die Form von *Achlya prolifera,* die in Hedströmmen lebt, unterscheidet sich teilweise von der von DE BARY beschriebenen Art, aber der Unterschied liegt in der Wachstumsart und in der vegetativen Entwicklung und dürfte standortsbedingt sein. So sind die Zotten, die früher mit einer Breite von 1/2—1 cm beschrieben worden sind, hier erheblich breiter. Im Hedströmmen erreichen die einzelnen Rasen, soweit sie nicht eine meterlange zusammenhängende Decke bilden, ungefähr Faustgrösse. Die Länge der Zotten hält sich um 3—4 cm, die Breite der Hyfen in den freien Zotten bis ungefähr 20 μ. Die Hyfen sind an den Enden leicht zugespitzt und sparsam verzweigt, wobei die Zweige in mehr oder minder rechten Winkeln von den Haupthyfen

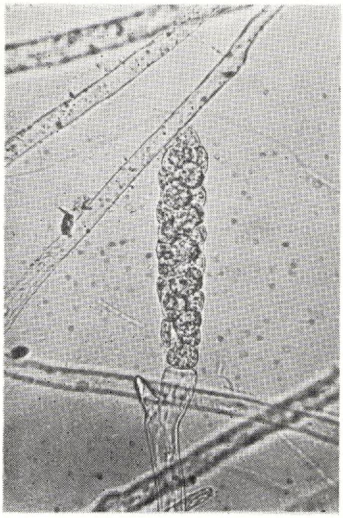

Foto 1.

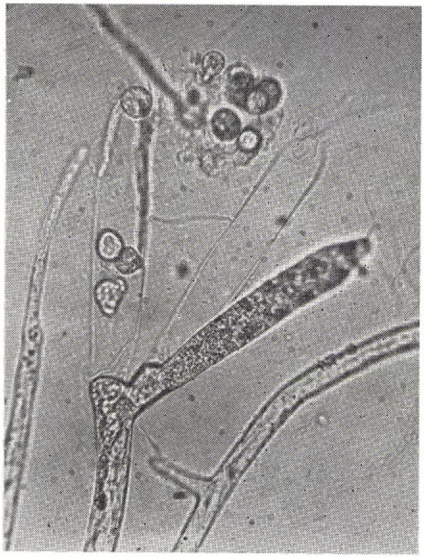

Foto 2.

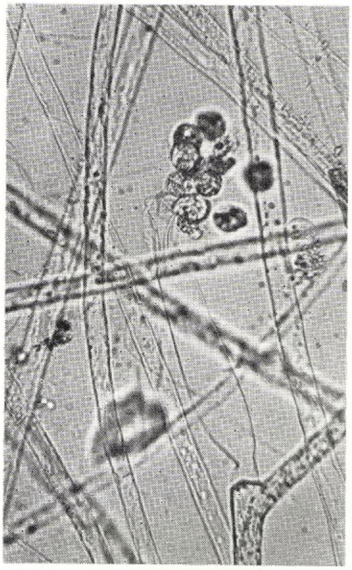

Foto 3.

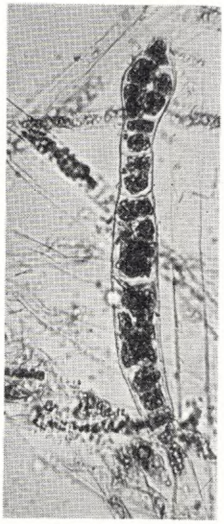

Foto 4.

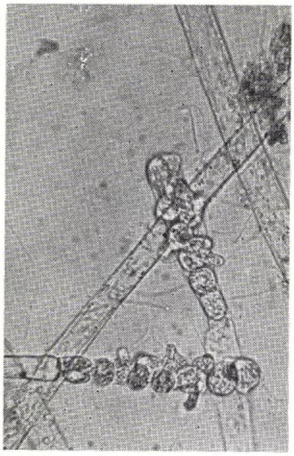

Foto 5.

Foto 1. Sporangium mit knospenförmiger Anlage eines neuen Sporangiums. — Vergr. ca 300 ×.
Foto 2. Ein Bündel von Sporangien mit Entleerung eines Sporangiums. — Vergr. ca 350 ×.
Foto 3. Entleertes Sporangium mit dem ausserhalb liegenden Sporenklumpen. — Vergr. ca 350 ×.
Foto 4. Atypische Sporenbildung. Ein Netzsporangium. -- Vergr. ca 350 ×.
Foto 5. Atypische Sporenbildung. Die Sporen keimen in dem Sporangium. — Vergr. ca 350 ×.

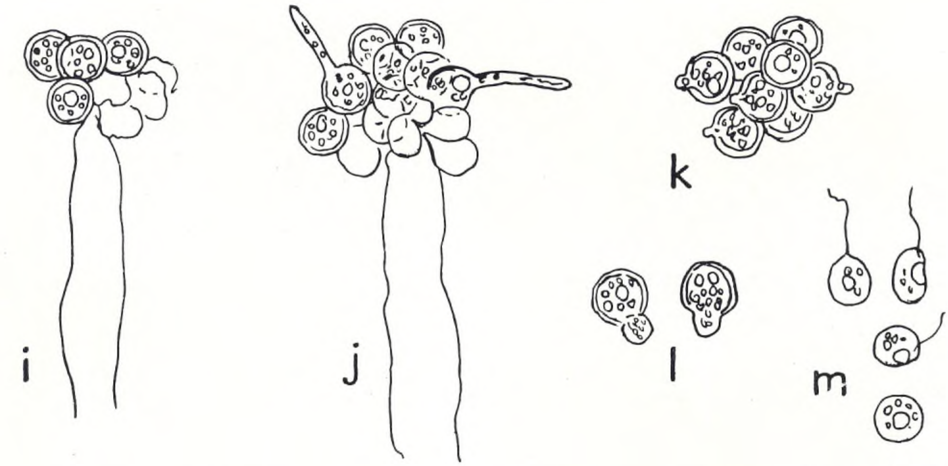

Abb. 3. Entleerte Sporangien und Bildung von Schwärmsporen. i. Sporenklump mit den zurückgebliebenen Membranen der ausgeschlüpften Sporen. j. In dem Sporenklump keimenden Sporen. k—m. Verschiedene Stadien der Schwärmsporenbildung.

ausgehen. An ihren Enden werden die keulenähnlichen Sporangien ausgebildet, und Zotten mit solchen Sporangien wurden reichlich auf Punkt 1 und 4 gefunden. Abb. 2, a—d, zeigen einige Sporangien in verschiedenen Entwicklungsstadien. Bei den Abb. 2 a und b, sieht man, wie der Inhalt der Hyfen sich an den Enden konzentriert, wobei sich eine Wand gegen den anderen Teil der Hyfe bildet. Unter dieser Wand bildet sich die Anlage eines neuen Sporangiums als eine kleine Knospe (Foto 1), der nach ihrer Reife ein Sporangium dritter Ordnung folgt. Ein solches kleines Bündel von Sporangien ist aus Foto 2 ersichtlich. In dem Sporangium teilt sich das Plasma später in Zoosporen auf, Abb. 2, c und d, die das Sporangium durch eine Öffnung an der Spitze verlassen. Die Ausleerung der Sporenmasse geschieht auf die für die Achlyagattung charakteristische Weise in einem Zuge, und die Sporen bleiben eine Zeit lang als ein Klumpen vor der Sporangienmündung liegen und umgeben sich da mit einer Wand. Der Diameter der Sporen ist 13—15 μ. Nach einiger Zeit schlüpfen sie aus ihren Wänden aus und schwärmen eine kurze Zeit als freie Zoosporen. Die Art hat also wie die meisten Achlyaarten nur ein Schwärmstadium. Auf dem Foto 2—3 sind Sporangien und Sporenklumpen zu sehen. und Abb. 3, i—m, zeigen den geschilderten Verlauf, soweit ich ihn an meinem Material beobachten konnte. In den Abb. 3, i und j, sieht man, wie das Sporangium nach der Entleerung zusammenfällt, sowie die als leere Hüllen in den Sporenklumpen zurückgebliebenen Sporenhäute. Es kommt vor, dass ein Teil der Sporen schon in dem Sporenklumpen keimt und das Schwärmstadium überspringt, ein Vorgang, der sich auch bei DE BARY abgebildet findet. Auf den Abb. 3, k und l, sieht man, wie die Sporen im Begriff stehen, in bewegliche Zoosporen

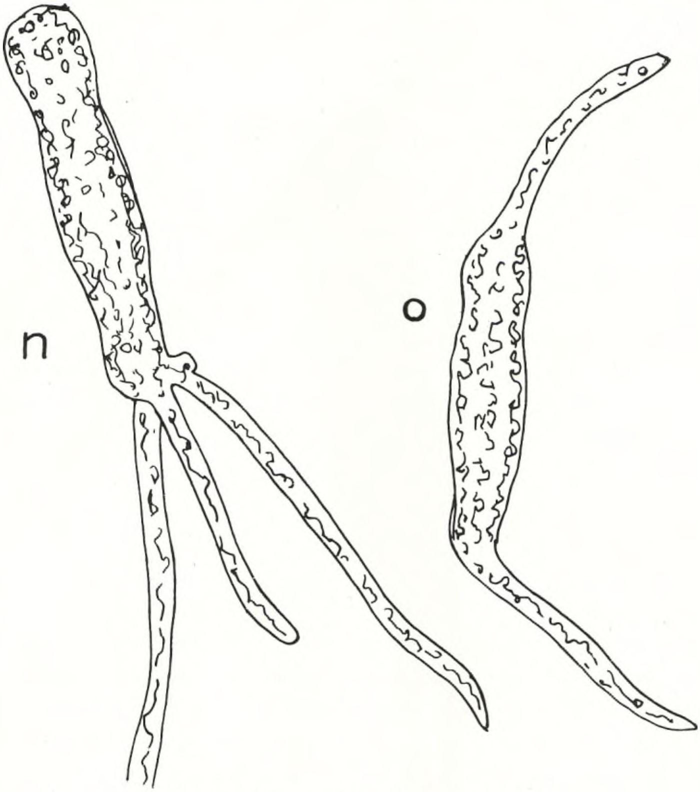

Abb. 4. Zu Gemmen umwandelte Sporangien.

überzugehen (Abb. 3 m). Ich habe indessen nur eine geringe Zahl beweglicher Zoosporen beobachtet und habe auch nicht mehr als eine Geissel auf jeder Spore sehen können, obwohl es nach DE BARYs Angabe zwei sein sollen. Auch DE BARY zeigt aber in seinen Abbildungen einige Zoosporen mit nur einer Geissel, die er als die jüngsten Individuen bezeichnet. In Abb. 3 m sieht man eine Spore, die nach dem Schwärmstadium zur Ruhe gekommen ist. Diese Ruheperiode geht dem Keimen zu einem neuen vegetativen Mycelium zuvor.

Der oben geschilderte Verlauf des Sporangien- und Sporenstadiums ist normal für frisches Pilzmaterial. Steht dieses aber einen Tag in Zimmertemperatur, so treten einige Hemmungserscheinungen ein, wie in den Abbildungen 2, e—h, abgebildet. In Abb. 2 e haben noch nicht alle Sporen das Sporangium verlassen, sondern die zurückgebliebenen haben sich mit einer Wand innerhalb des Sporangiums umgeben. Nach COKER können sie nach einer Zeit ihre Wände durchbrechen und in dem Sporangium umherschwimmen, bis sie aus der Öffnung an der Spitze herausfinden. In Abb. 2, f und g, sowie auf Foto 4 sieht man einige sogenannten Netzsporangien, ähnlich den, die normalerweise bei einer anderen Saprolegniacéengattung, Dictyuchus, vorkommen. Die Sporen treten da einzeln durch Öffnungen an den Seiten des Sporangiums aus, wobei sie ihre Hüllen wie ein Netzwerk in dem Sporangium zurücklassen. In Abb. 2 h, schliesslich, zeigt sich ein Sporangium von sog. *Aplanes*typus, eine Bezeichnung, die auf die Art *Achlya aplanes* MAURIZIO zurückgeht, bei der kein Zoosporenstadium vorkommt, sondern die Sporen direkt entweder schon innerhalb des Sporangiums keimen, wie Abb. 2 h zeigt und wie sich aus Foto 5 ergibt, oder in dem Sporenklumpen ausserhalb des Sporangiums, wie Abb. 3 j zeigt. COKER erwähnt auch, dass die Sporen bei den *Achlya*arten eine starke Tendenz haben, innerhalb der Sporangien zurückzubleiben und in Zusammenhang mit verschlechterten Milieuverhältnissen unmittelbar zu keimen. Werden die Lebensbedingungen noch schlechter, tritt die Bildung von sog. Gemmen ein. Stücke von veränderten, verdickten und aufgeschwollenen Hyfen sowie vor allem von Sporangienanlagen, die in ihrer Entwicklung gehemmt wurden, werden abgeschnürt und wachsen zu neuen Hyfen aus. Abb. 4, n und o, zeigen einige solche Gemmen.

Die Organe des sexuellen Vermehrungsverlaufs, bestehend aus Antheridien und Oogonien, wurden bedeutend seltener als die Sporangien angetroffen. Bei der ersten Probeentnahme wurden einige Zotten mit Oogonien und Antheridien im Wasserlauf bei Punkt 2, und bei der zweiten Probeentnahme bei Punkt 4 gefunden. An der letzteren Stelle, wo das Material ungewöhnlich rein, d.h. frei von Eisenausscheidungen und Schlammpartikeln war, konnte man einen deutlichen Unterschied in den Zotten feststellen, und zwar zwischen einem dunkleren schleimigeren, inneren und einem helleren, festeren, äusseren Teil, in dem die Sporangien sassen. In den inneren Teilen, in denen die Hyfen schlaffer und verflochtener waren, fanden sich reichlich sexuelle Reproduktionsorgane. Die meisten Oogonien wachsen terminal auf langen Seitenzweigen zu den Haupthyfen, in geringerer Menge wachsen sie interkalar und dann manchmal in Reihen hinter einander. Die Wachstumsweise unterscheidet sich hier von der von DE BARY geschilderten, der von Oogonien auf kurzen Stengeln, deutlich traubenförmig angeordnet, spricht, die nach seiner Angabe in grosser Zahl an den Haupthyfen vorkommen. Die Oogonien sind gewöhnlich rund, nur die interkalaren manchmal langgestreckt oder von unbestimmter Form. Ihre Breite variiert zwischen 40 und 80 μ, hält sich aber im allgemeinen zwischen 50 und 60 μ. Die Wände der Oogonien sind glatt, und ich habe nicht die von DE BARY erwähnten Poren wahrnehmen können. Auch v. MINDEN (1911) beschreibt in der Flora der Mark Brandenburg die Oogonien »mit glattem Membran« und sagt, dass die Poren »scheinbar oft gar nicht vorhanden« sind. Die Zahl der Oosporen hält sich meist zwischen 4 und 5, ich habe aber auch Oogonien mit bis zu 12 Oosporen gesehen. Diese haben eine Grösse von 21 bis 26 μ im Diameter und sind excentrisch, d.h. die im Plasma eingeschlossene Fettkugel ist etwas an die Periferie verschoben. Die Antheridien wachsen wie die Oogonien meist

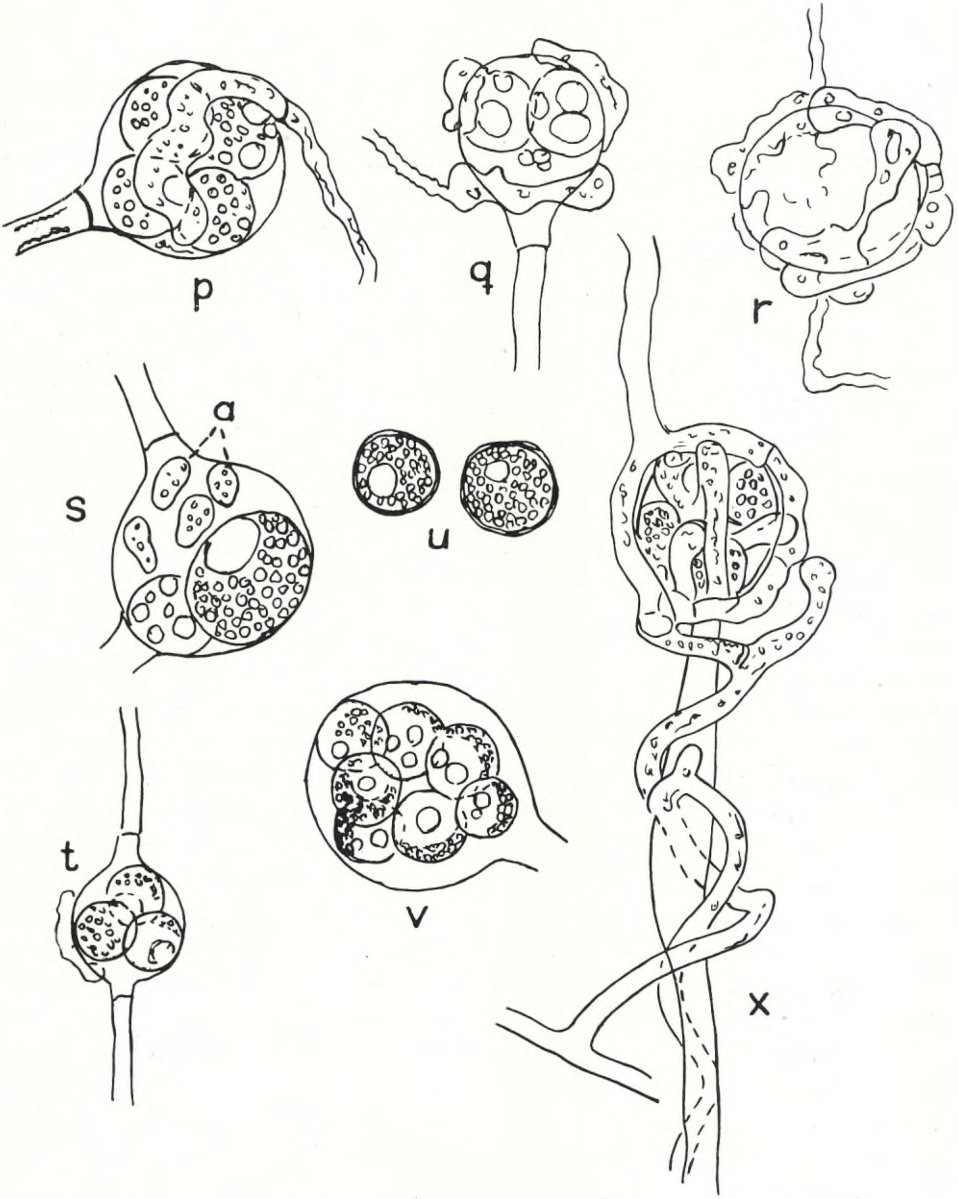

Abb. 5. Die Befruchtung und die Oosporenbildung: p—r und x. Von Antheridien umschlungene Oogonien. s. Ein Oogonium mit beweglichen Sporen (a). t. Interkalares Oogonium. u—v. Oosporen.

terminal auf langen, dünnen, reich verzweigten Hyfen, die von anderen Haupthyfen als den der Oogonienstengel ausgehen und also von diklinischem Ursprung sind. Diese Antheridienstengel sind in ihrer ganzen Länge in dem verworrenen Mycelium schwer zu beobachten, besonders da sie leicht zu zerfliessen und sich nach der Befruchtung der Oogonien zu einer konturlosen Masse rings um diese herum aufzulösen scheinen. Ich habe indessen in keinem einzigen Fall feststellen können, dass die antheridietragenden Zweige von denselben Hyfen wie die Oogonien ausgehen. Ihrer Form nach sind die Antheridien langgestreckt, oft gelappt, und legen sich mit ihrer ganzen Langseite um das Oogonium. Oft ist dieses fast ganz bedeckt mit einer Mehrzahl von Antheridien, deren Stiele, wie ich gesehen habe, sich windenartig um die Stengel der Oogonien schlingen können.

Die Abb. 5, p—x, zeigen eine Anzahl Oogonien im Verlauf der Befruchtung. In Abb. 5 s sieht man eine schon von CIENKOWSKI (1855) erwähnte Erscheinung, die darin besteht, dass die Oosporen sich in dem Oogonium zu einer Art beweglicher Zoosporen umbilden können, wobei die Oospore sich zuerst erheblich vergrössert. Die mit a bezeichneten Oosporen befanden sich in lebhafter Bewegung. Die Fotos 6—10 zeigen ebenfalls den Befruchtungsverlauf. Auf Foto 6 ist deutlich ein Bündel von Antheridien zu sehen, die das noch nicht reife Oogonium umschlingen. Auf dem Foto 7 und 8 sieht man, wie die langgestreckten Antheridien sich den Oogonienwänden entlang gelegt haben, und auf Foto 7 wird ein Befruchtungsschlauch oben schwach sichtbar. Foto 9 und 10 zeigen einige Oogonien mit gut sichtbaren excentrischen Oosporen.

Obige Charakteristik des Pilzes stimmt — mit der bereits erwähnten Modifikation der Wachstumsart — mit den von DE BARY und später v. MINDEN gegebenen Beschreibungen der *Achlya prolifera* gut überein. Als eine neue Form der Art möchte ich sie noch nicht bezeichnen. Es ist natürlich möglich, dass man bei Reinzüchtung der Art weitere Merkmale feststellen kann, die vielleicht von denen abweichen, die bisher bei dem Pilz im Naturzustande beobachtet werden konnten, und dann kann sich möglicherweise ergeben, dass es sich um eine neue Art handelt. Einstweilen mag der Pilz indessen mit dem Namen der *Achlya*art bezeichnet werden, mit der er in den meisten, für die Bestimmung wichtigen Einzelheiten übereinstimmt.

Es erhebt sich nun die Frage, wie sich das Massenauftreten des Pilzes in dem erwähnten Wasserlauf erklären lässt. Normalerweise scheinen die *Achlya*arten in feuchtem Boden und in kleineren Gewässern, besonders in Waldtümpeln, Torfstichen und anderen stillen Wassern mit reinem und klarem Wasser zu leben. Besonders Gewässer, die von Bäumen umgeben sind, und in denen sich Zweige und andere Holzabfälle sammeln, scheinen günstige Entwicklungsmöglichkeiten für viele *Achlya*arten zu bieten. Mehrere sind auch auf toten Insekten und Fischen im Wasser gefunden worden. Bezüglich des Vorkommens von *Achlya*arten in verunreinigtem Wasser hat HARVEY (1952) einige interessante Beobachtungen gemacht. Er isolierte eine Anzahl Saprolegniacéen, darunter 4 *Achlya*arten, von mehreren Gewässern in Ohio, U.S.A., die teilweise von städtischem Abwasser stark verunreinigt waren. In keinem Fall erhielt er eine *Achlya* aus einem stärker, und nur selten eine

Foto 6.

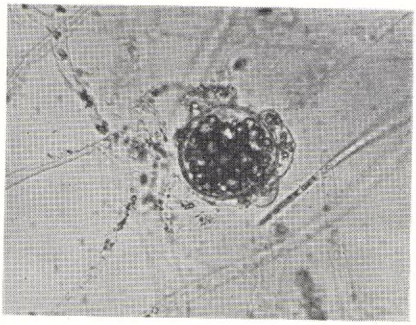

Foto 7.

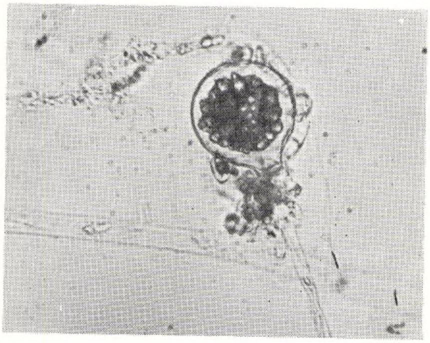

Foto 8.

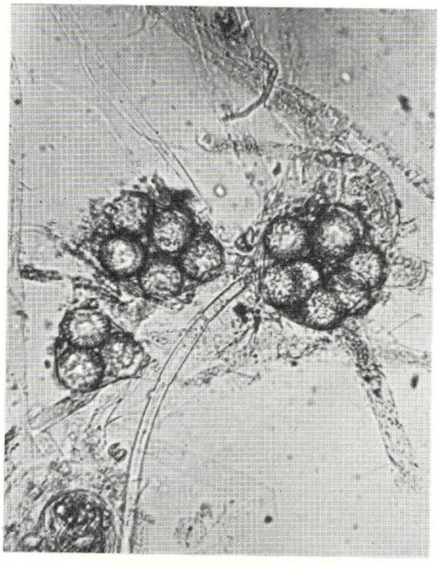

Foto 9.

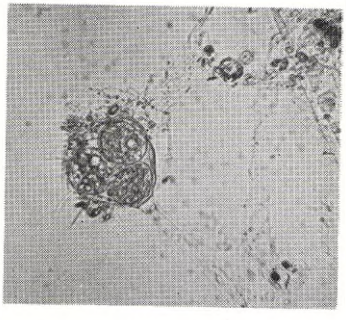

Foto 10.

Foto 6. Ein von zahlreichen Antheridienzweigen umschlungenes Oogonium. — Vergr. ca 300 ×.

Foto 7. Die Befruchtung. Oogonium mit Antheridien. — Vergr. ca 350 ×.

Foto 8. Die Befruchtung. Oogonium mit Antheridien. — Vergr. ca 300 ×.

Foto 9. Oogonien mit Oosporen. Vergr. ca 350 ×.

Foto 10. Oogonium mit deutlich excentrischen Oosporen. — Vergr. ca 350 ×.

aus schwach verunreinigtem Wasser. Bei einer grossen Zahl von Proben wurde das weitaus grösste *Achlya*vorkommen in reinem Wasser festgestellt.

Geeignete natürliche Standorte für die *Achlya prolifera* im Hedströmmen gibt es in der waldreichen Umgebung des Flusses reichlich. Von dort aus können die Oosporen, die eine lange Ruhezeit — für *Achlya prolifera* 212 Tage — haben, mit dem Schmelzwasser des Frühjahrs in den Fluss hineingespült worden sein, wo sie zur Zeit des Keimens in dem durch das Abwasser der Wallboardfabrik gedüngten Wasser geeignete Temperatur- und Nahrungsverhältnisse fanden. Für *Leptomitus lacteus* hat SCHIKORA (1897) solche Entwicklungsverhältnisse nachgewiesen. Es liegt im übrigen nahe, das Auftreten der *Achlya prolifera* mit dem des viel untersuchten und wohlbekannten *Leptomitus lacteus* zu vergleichen, der, wie bereits erwähnt, im Hedströmmen ebenfalls, wenngleich in bedeutend geringerer Zahl gefunden wurde. Hier sollen nur in Kürze einige Versuche wiedergegeben werden, die zur Klarlegung der Nahrungsbiologie dieses Pilzes gemacht wurden:

TROMMSDORFF (1918) fand nach zahlreichen Züchtungsversuchen mit *Leptomitus* in einer Stammlösung von Nährsalzen mit einem Zusatz von Pepton, unorganischen Stickstoffverbindungen und Rohrzucker folgendes:

1. *Leptomitus* wächst nicht in Lösungen von Zucker ohne Zusats von Stickstoff.
2. Er wächst üppig in Lösungen von hochmolekylaren Eiweisstoffen unabhängig davon, ob Zucker zugesetzt wird oder nicht.
3. Er wächst schwach in Lösungen mit nur unorganischen Stickstoffsalzen, gut dagegen, wenn einer solchen Lösung Zucker zugesetzt wird.

TROMMSDORFF zieht daraus den Schluss, dass die Bedeutung der Kohlenhydrate für den *Leptomitus* darin liegt, dass sie das Wachstum des Pilzes in den Fällen fördern, in denen keine anderen Stickstoffverbindungen als unorganische vorhanden sind. Gewässer, die einen starken Zuschuss von organischer Substanz empfangen, bieten die besten Lebensmöglichkeiten für den *Leptomitus*. Dieser kann aber eine reiche Entwicklung auch an Stellen mit fortschreitender Mineralisierung oder in Gewässern mit überwiegend anorganischem Stickstoff zeigen, wenn sich nur genügend Kohlenhydrate vorfinden.

TIEGS (1938) behauptet, dass die vornehmste Nahrungsquelle für den *Leptomitus* in organischen Stickstoffverbindungen besteht und dass der Zuwachs durch das Vorhandensein von Zuckerarten gefördert wird. Die Entwicklung des Pilzes geschieht nach seiner Angabe am besten bei niedriger Temperatur und saurer Reaktion mit einem optimalen pH-Wert von 2,9—5,4. Bezüglich der letzten Angabe betont er, dass sie für den Pilz in Reinkultur gilt und dass diese Verhältnisse nicht unbedingt mit den natürlichen in den Gewässern verglichen werden können, wo die zuwachsfördernden und -hemmenden Faktoren so viel zahlreicher und oft unbekannt sind.

SCHADE (1940) stellte einen Züchtungsversuch mit *Leptomitus lacteus* und zum Vergleich auch mit der ihm nahe stehenden *Apodachlya brachynema* HILD. an, die in ähnlichen Gewässern mit reinem Wasser wie *Achlya prolifera* lebt. Als Medium für seine Stammkultur benutzte er Peptongelatine mit Zusatz von Glykose. Die optimale Temperatur für die Entwicklung der Pilze in den Stammkulturen war 19—25°, der optimale pH-Wert 6,0, wobei sich eine Sauerstoffzufuhr als notwendig erwies. Einige seiner Untersuchungsresultate zählt er, wie folgt, auf:

Beide Arten sind imstande, Sulphate zu reduzieren und so ihren Bedarf an Schwefel zu decken.

Nitrat und Ammonium sind für keinen der Pilze geeignete Stickstoffquellen.

Nur gewisse Aminosäuren sind für beide Arten geeignet, darunter d,1-Alanin, 1-Leucosin. *Apodachlya* wächst auf d-Leucosin, *Leptomitus* dagegen nicht. Keine der Arten wächst auf Glycin, Metylamin, Acetamid oder Asparagin.

Glycin und Asparagin kann von beiden Arten verwertet werden, wenn Acetat vorhanden ist.

Zuckerarten sind für *Leptomitus* als Nahrungssubstrat ungeeignet, *Apodachlya* aber wächst gut auf Dextrose, Levulose und Saccarose, nicht dagegen auf Galaktose und Maltose.

Über die Oekologie der *Achlya*arten sind Angaben in der Literatur sehr selten. Aus Dänemark hat LUND (1934) einige Erfahrungen über das Verhältnis dieser Arten zu Temperatur, Sauerstoffgehalt und pH an den natürlichen Standorten mitgeteilt. Als Beispiel nennt er, dass an einem heissen Julitag nur wenige Phycomyceten an einer Stelle gefunden wurden, wo sie im Mai noch sehr zahlreich waren. Die reichste Entwicklung an sexuellen Reproduktionsorganen bei der *Achlya* fand er im Frühling. Die *Achlya* braucht weiter eine gute Sauerstoffzufuhr. In der Natur gedeihen diese Pilze deshalb am besten auf Gegenständen, die auf dem Wasser fliessen sowie auf flachen Stellen und auf Stellen, wo das Wasser in Bewegung ist. Diese Beobachtungen stimmen gut mit denen überein, die hinsichtlich der *Achlya prolifera* gemacht wurden. Über das Verhältnis der *Achlya*arten zum Säuregrad des Wassers meint LUND, sie seien ziemlich indifferent d.h. nicht besonders empfindlich für Veränderungen des pH-Wertes.

Schliesslich sei eine Untersuchung von PIETERS (1915) über das Verhältnis zwischen Zuwachs und Vermehrung bei einigen Saprolegniacéen, u.a. gerade der *Achlya prolifera,* erwähnt. Von Stammkulturen des letztgenannten Pilzes auf Erbsenagar wurde dieser in Medien, bestehend aus Pepton von 0,01 —0,03 % Lösung, Pepton mit einer der Zuckerarten Dextrose, Levulose, Maltose oder Saccarose in verschiedenen Verdünnungen sowie in die letztgenannten Medien mit einem Zusatz von Nährsalzen (Phosfaten, Sulphaten und Nitraten) überführt. PIETERS kam zu dem Ergebnis, dass der Pilz in den zwei erst genannten Medien gut wuchs. Der Zusatz von Nährsalzen, besonders Sulphaten steigerte den Zuwachs und das Vermehrungsvermögen deutlich, nicht jedoch in dem Medium, das Levulose enthielt. Diese Zuckerart wirkte im Gegensatz zu Maltose und Dextrose auf den Zuwachs nicht fördernd ein. Weiter weist er darauf hin, dass Saccarose wahrscheinlich von dem Pilz nicht eher aufgenommen wird, als sie mit Hilfe einer Enzyme invertiert wird.

Um einige Schlüsse bezüglich der Faktoren, die in erster Linie zu der enormen Entwicklung der *Achlya prolifera* im Hedströmmen beitragen, ziehen zu können, müssen wir in etwa die chemischen Verhältnisse des Flusses und die Einwirkung des Abwassers betrachten. Oberhalb der Wallboardfabrik hat der Hedströmmen einen oligotrophen, durch reines und klares Wasser gekennzeichneten Charakter. Wie ich erfahren habe, gibt es in dem Teil des Flusses, der oberhalb der Probeentnahmestellen liegt, keine Kloakeinmündungen. Es dürfte deshalb ausschliesslich das Abwasser der Fabrik sein, auf dem der besondere und dazu sehr kräftige Nahrungszuschuss im Flusse beruht. Gemäss einer Untersuchung von BERLING (1955) über die chemische Zusammensetzung des Abwassers von Fabriken, die Fiberplatten herstellen, besteht dieses zu etwa 6 ⁰/₀ aus gelösten Holzstoffen (insbesondere Hemicellulosen). Zu 50—60 ⁰/₀ besteht die gelöste organische Substanz aus Zuckern (Pentose, Mannose), der Rest setzt sich vornehmlich aus Essigsäure, wasserlöslichen Zellinhaltsstoffen sowie Ligninzersetzungsprodukten zusammen. Nach einer Berechnung vom April 1956 folgen mit dem Abwasser der Wallboardfabrik in Skinnskatteberg 39 gr/l gelöste Bestandteile. Die totale Menge des Abwassers beträgt ca 75 l/min, und der Fluss nimmt so an gelösten Holzbestandteilen ca 2,9 kg/min. entgegen. Die Folge davon ist, dass das Abwasser einen sehr hohen Sauerstoffverbrauch, nach BERLINGs Berechnung mit Werten von 2000—2200 mg/l Kaliumpermanganatverbrauch per Gram organischer Substanz, hat. Mit dem Abwasser folgt weiter, wenigstens zeitweise, ziemlich viel Fiberabfall, der sich in dem dafür aufgeführten Schlammbecken nicht absetzen konnte.

Die unten stehenden Tabellen zeigen einige Werte für die chemische Zusammensetzung teils des Abwassers der Fabrik bei einer Untersuchung aus dem Jahre 1943, teils des Hedströmmen unterhalb der Fabrik bei Untersuchungen in der zweiten Hälfte des Jahres 1956. Zum Vergleich habe ich auch einige Werte für den See Övre Vettern, der oberhalb des Hedströmmen liegt, aufgenommen.

Tab. I. Die chemische Zusammensetzung des Abwassers der Wallboardfabrik in Skinnskatteberg an 29/10 1943.

Temperatur bei Probeentnahme. C°	21,0
Permanganatverbr. $KMnO_4$, mg/l	7300
Fibergehalt mg/l	410
Reaktion pH, el.Kol.	4,66
Gel. Sauerstoff O_2 mg/l	0
Biochem. Sauerstoffverbr. mg/l	1850

Tab. II. Die chemische Zusammensetzung des Wassers vom Hedströmmen am 4/7 und am 13/12 1956.

	A	B	C	D
Temperatur bei Probeentnahme, C°	18,2	18,0	< 10	< 10
Farbe, mg/l Pt			35	30
Trübung, °ZP.10^5	150	1770	schwach	deutlich
Permanganatverbr. $KMnO_4$, mg/l	44	200	96	100
Reaktion pH, el.Kol.	6,1	5,9	6,2	6,1
Gel. Sauerstoff, O_2 mg/l	7,8	4,1	9,9	9,2

Kol. A: Övre Vettern ca. 500 m oberhalb des Auslaufs in den Hedströmmen am 4/7.
Kol. B: Der Hedströmmen unterhalb der Fabrik bei Punkt 2 am 4/7
Kol. C: » » » » » » » 2 » 13/12.
Kol. D: » » » » » » » 4 » 13/12.

Wie aus der Tabelle II ersichtlich, wirkt das Abwasser der Fabrik deutlich auf die Wasserbeschaffenheit des Hedströmmen ein. Dieses geht am besten aus den Zifferwerten während des Sommers am Punkt 2 sowohl für die Trübung als auch für den Permanganatverbrauch hervor, der um diese Zeit das Normale, wie es der Wert des Övre Vettern repräsentiert, um das vierfache überschreitet. Der entsprechende niedrige Wert für den Sauerstoffgehalt bestätigt dieses Verhältnis. Eine vom Laboratorium der Fabrik am 13/12 vorgenommene Untersuchung zeigt in den Kolonnen C und D die Wasserbeschaffenheit im Spätherbst, in dem der Pilz seine üppigste Entwicklung aufweist. Leider waren keine genauen Temperaturwerte zu erhalten, aber aus den vorliegenden Ziffern kann man einen niedrigen Temperatur, einen guten Gehalt an gelösten organischen Bestandteilen, eine schwach saure Reaktion und eine grosse Menge von gelöstem Sauerstoff ablesen.

Es ist offenbar, dass ein oder einige bestimmte oekologische Faktoren des Wassers die Hauptursache für die Entwicklung des *Achlya*pilzes in dem grösseren Teil der berührten Strecke des Hedströmmen sind. Die eigentümliche Erscheinung, dass sie in dem unteren Teil der Stromstrecke so gut wie ganz fehlt und dass an ihrer Stelle dort *Leptomitus* auftritt, deutet auf eine gewisse Ungleichheit im Milieuanspruch dieser beiden Arten hin, die vielleicht teilweise mit den Ergebnissen der oben zitierten Untersuchungen über die Oekologie dieser beiden Arten erklärt werden kann. Betreffend des *Leptomitus* ist allgemein festgestellt worden, dass er in seiner Entwicklung von dem Vorhandensein von vor allem hochmolekylaren Stickstoffverbindungen abhängig ist. Da dem Fluss weder mit Kloakabwasser noch mit Fabrikabwasser ein besonderer Zuschuss an diesen Stoffen zugeführt wird, muss *Leptomitus* seinen Stickstoff aus dem Fluss selbst erhalten. In der geringen Wassermenge des abgesperrten unteren Teil des Flusses findet sich die grösste Koncentration von Zersetzungsprodukten organischer Stoffe, die dem Wasser von den Ufern und dem Boden zugeführt werden. Offenbar genügt der Zugang an organischem Stickstoff und wirkt der besondere Zuschuss der Zuckerarten des Fabrikabwassers zusätzlich stimulierend dahin, dass *Leptomitus* in diesem Teil des Flusses begünstigt wird. In dem übrigen Teil des Flusses, in dem der Zugang an organischem Stickstoff auf Grund der grösseren Verdünnung bedeutend geringer ist, fand sich kein Leptomitus sondern ausschliesslich Achlya prolifera, die hier offenbar das für ihre Entwicklung vorteilhafteste Milieu gefunden hatte. Dass dies nicht darauf beruhen kann, dass die *Achlya* Eiweisstoffe scheuen sollte, ergibt sich aus früheren Fundes des Pilzes auf toten Tieren im Wasser und aus PIETERS Untersuchungen. Leider hat dieser Forscher nicht untersucht, wie sich der Pilz bei einseitiger Ernährung mit hauptächlich Zuckerarten verhält. Dass eine solche Nahrungszusammensetzung für *Leptomitus* ungeeignet ist, haben, wie oben ausgeführt, sowohl TROMMSDORFF als auch SCHADE nachgewiesen. Die Beobachtung des Letzteren über die abweichende Reaktion der *Apodachlya* in dieser Nahrungsfrage lädt zu einem Vergleich dieser mit der *Achlya prolifera* im Hedströmmen ein. Es ist möglich, dass gerade der hohe Gehalt an einfachen Zuckerarten wie Pentose und Mannose, die mit dem Abwasser in den Fluss kommen, den wichtigsten Nahrungsfaktor für eine Massenentwicklung dieser Art bildet. Diese wird weiter von anderen, für die Art wichtigen, oekologischen Faktoren begünstigt, die im Hedströmmen, besonders während des Winterhalbjahres herrschen, wie niedrige Temperatur, schwach saure Reaktion, sowie genügender Zugang an Sauerstoff. Eine grössere Klarheit über den neuen Abwasserpilz, dessen Physiologie und auch dessen Systematik dürfte nur seine Reinzüchtung und eine Untersuchung über sein Verhältnis zur Nahrung von verschiedener Beschaffenheit ergeben können.

Zum Schluss ein kleiner Hinweis auf die *Achlya*arten, der aus dem Gesichtspunkt des Fischereischutzes von Interesse sein kann: Zwei amerikanische Forscher, TIFFNEY und WOLF (1937), fanden, dass eine, der *Achlya prolifera* nahe stehende Art, *Achlya flagellata,* als Parasit auf Fischen vorkommen kann, und dass diese 1936 eine schwere Epidemie mit folgendem Massensterben des Laichs von amerikanischen Bachsaiblingen (Salvelinus fontinalis) verursacht hat.

Zusammenfassung

Der Aufsatz behandelt ein Massenauftreten der Saprolegniacéenart *Achlya prolifera* DE BARY als Abwasserpilz, das im Fluss Hedströmmen im Västmanland unterhalb einer Fabrik, die Holzfaserplatten herstellt, im November 1956 beobachtet wurde. Da eine solche Beobachtung für irgend eine der Gattung *Achlya* zugehörige Art bisher noch nicht mitgeteilt ist, wurde der gefundenen Art eine ausführlichere Beschreibung ihrer Morphologie und ihres Auftretens in diesem Wasserlauf unter Hinzufügung einiger historischer Daten gewidmet. Zum Schluss wird versucht, eine Erklärung für dieses

Massenauftreten zu finden und zwar teils auf Grund einer Reihe von Versuchen einiger Forscher über die Nahrungsbiologie dieser und ihr nahe stehender Arten, teils auf Grund der oekologischen Verhältnisse, die im Hedströmmen zur Zeit der Untersuchung herrschten.

Die wichtigsten Ergebnisse der Untersuchung können, wie folgt, zusammengefasst werden:

Die Art tritt in dem Wasserlauf in der gleichen Weise wie andere bekannte Abwasserpilze, z.Bsp. *Sphaerotilus,* auf. Sie scheint hauptsächlich in den Teilen des Flusses, in denen die Wasserzuführung reichlich und die Lüftung gut ist, vorzukommen. In einem unteren, teilweise trockengelegten Teil des Flussbettes war die Art fast völlig verschwunden und durch den Abwasserpilz *Leptomitus lacteus* ersetzt.

In den für die Artbestimmung wichtigen morphologischen Eigenschaften stimmt die gefundene Art wohl überein mit der von DE BARY in der zweiten Hälfte des achzehnten Jahrhunderts ausführlich beschriebenen Art *Achlya prolifera* mit der Ergänzung über das Aussehen der Oogonienwände, die später von v. MINDEN gemacht wurde. Die Abweichungen der im Hedströmmen gefundenen Art von den erwähnten früheren Beschreibungen der *Achlya prolifera,* besonders betreffend ihrer Wachstumsweise, dürften milieubedingt sein.

Die wichtigste Nahrungsquelle für den Pilz scheint der grosse Gehalt des Fabrikabwassers an gelösten einfachen Zuckerarten zu sein, die dem Hedströmmen kontinuierlich zugeführt werden. Da Eiweisstoffe dem Fluss wahrscheinlich so gut wie vollständig fehlen, können diese für die *Achlya prolifera* nicht annähernd die gleiche Bedeutung haben wie für den *Leptomitus lacteus.*

Eine Reinzüchtung des gefundenen Pilzes sowie ein Versuch mit verschiedenen Nahrungssubstraten dürften eine vollständigere Kenntnis seiner Systematik und Nahrungsphysiologie sowie eine Erklärung für sein Massenauftreten geben können.

Literaturverzeichnis

APINIS, A. 1930. Untersuchungen über die in Lettland gefundenen Saprolegniacéen etc. *Acta Horti Bot. Univ. Latv., 4: 201—246.*

ARESCHOUG, J. E. 1845. Beobachtungen über die merkwürdige Pilze *Achlya prolifera. Hornchuch's Arch. f. Skand. Beitr. zur Naturgesch. I Th: 170—172.*

BARY, A. DE 1852. Beitrag zur Kenntnis der *Achlya prolifera* NEES. *Bot. Zeit. 10: 473, 489 u. 505.*

— 1881. *Abh. Senck. Naturf. Ges. 12: 225.*

— 1888. Species der Saprolegniacéen. *Bot. Zeit. 46: 597, 613, 629 u. 645.*

BERLING, K. 1955. Chemische Veränderungen des Holzes beim Defibratorverfahren und die chemische Zusammensetzung der Abwässer von Holzfaserplattenwerken. *Das Papier 9 (17/18): 441.*

CARUS, C. G. 1823. Beitrag zur Geschichte der unter Wasser an verwesenden Thierkörpern sich erzeugenden Schimmel- oder Algengattungen. *Nova Acta Academ. C. L. C. N. C., 11, Th. 2: 491.*

CIENKOWSKI, I. 1855. Algologische Studien: (3). *Achlya prolifera* NEES. *Bot. Zeit. 13: 801.*

COKER, W. C. 1923. The Saprolegniaceae with notes on other water molds: 116—118. *Univ. of N. C. Press, Chapel Hill.*

— and MATTHEWS, V. D. 1937. Saprolegniales in *N. A. Flora, 2 (1): 1—76.*

GÄUMANN, E. 1918. Ein Beitrag zur Kenntnis der lappländischen Saprolegniacéen. *Botaniska Notiser för 1918: 151.*

HARVEY, J. V. 1952. Relationship of aquatic fungi to water pollution. *Sew. and ind. wastes 24: 1159—1164.*

KOLKWITZ, R. 1950. Oekologie der Saprobien. *Schriftenreihe des Vereins f. Wasser- Boden- und Lufthygiene Nr 4.*

LIEBMANN, H. 1951. *Handbuch der Frischwasser- und Abwasserbiologie. Band 1.*

LUND, A. 1934. Studies on danish freshwater Phycomycetes. *De Kgl. Danske Vidensk. Selsk. Skrifter, Nat. og Mat. Avd. 9. Række VI, 1.*

v. MINDEN, M. 1911. Saprolegniineae in *Kryptogamenflora von Mark Brandenburg 5, 1.*

PETERSEN, H. E. 1909. Studier over Ferskvands-Phykomyceter. *Botanisk Tidskrift 29: 345.*

PIETERS, A. J. 1915. The relation between vegetative vigor and reproduction in some Saprolegniaceae. *Am. Journ. of Botany. 2: 529—576.*

SCHADE, A. L. 1940. The nutrition of *Leptomitus. Am. Journ. of Botany 27: 376—384.*

SCHIKORA, F. 1899. Entwicklungsbedingungen einiger abwässerreinigender Pilze, insbes. *Sphaerotilus fluitans* nov. spec. und *Leptomitus lactus* AG. *Zeitschr. f. Fischerei und deren Hilfswissensch. 7: 1.*

TIFFNEY, W. N. and WOLF, F. T. 1937. *Achlya flagellata* as a fish parasite. *Journ. of Elisha Mitch. Soc. 53: 298—300.*

TROMMSDORFF, R. 1918. Ueber die Wachstumsbedingungen der Abwasserpilze *Leptomitus* und *Sphaerotilus. Centralbl. f. Bakt. Abt. 2, Bd. 48.*

The Coregonid Problem. VI. The Palearctic species and their intergrades

By Gunnar Svärdson

Contents

1. Introduction

Whitefish and ciscoes have been well-known for their complicated variation for a long time. No agreement among the systematists on how to interpret the variation in these fish has so far been reached.

There must be something peculiar to the whitefish (which are more variable in Palearctic than the ciscoes, while the opposite is true in Nearctic), which is responsible for this variation. But though these fish have been the subject of extensive taxonomic investigations, no clue to their peculiarity has been found.

The bulk of the whitefish populations live in the U.S.S.R. and BERG (1948) as well as PRAVDIN (1954) and others have made extensive research into the morphology and ecology of the local populations. The important economic value of these fish has been a further stimulus for this research, apart from the taxonomic and evolutionary impetus. The Russian work has brought a mass of data to light, but no interpretation of the nature of the variation. BERG, as well as PRAVDIN, have used a rather traditional species concept with concentration on the morphological approach. Less weight has been laid on the ecology and no distinction has been made between the genetical as opposed to nongenetical background of the phenotypic appearance of the fish.

West of the U.S.S.R. THIENEMANN and WAGLER have studied the Alpine and JÄRVI the Finnish whitefish populations. THIENEMANN adopted the method suggested by **Nüsslin** of separating whitefish populations by their gillraker numbers, while **Wagler** was a pioneer in showing the importance to taxonomy of the ecology of the fish.

They were both led into a paradoxal situation, as **Thienemann** found the gillrakers fundamental in taxonomy but nevertheless thought them to be environmentally modified, while **Wagler** stressed the importance of growth rate in the identification of the various species though all authors knew very well, as also **Wagler** himself, that the growth of the whitefish could be altered to a high degree by the abundance of food and the density of the fish population.

Steinmann (1950—51) also studied the Alpine whitefish populations and tried to apply the modern ideas of polytypic species. He then found that the evolution of all the species was probably sympatric and postglacial which was at variance with the theory of the importance of geographical isolation as well as the rapidity of evolution (**Mayr** 1942, **Svärdson** 1949, **Brooks** 1950).

Common to several of these students of whitefish was the belief that the fish displayed some special "plasticity" or unusual rapidity of evolution, which was the explanation for the impossibility of pidgeonholing them into proper species and subspecies.

The interpretation, given in this paper, is in conformation with the general ideas of speciation which have been evolved during the last decades of fruitful amalgamation between genetics, ecology, ethology and systematics, often called the study of evolution.

The main point is that a number of whitefish species has evolved allopatrically during geographical isolation. After the breakdown of this isolation the forms have secondarily obtained contact and were then capable of living sympatrically, as species. No sterility barrier, however, had evolved and secondary introgression between the species therefore occurred, very slightly in great lakes but rather extensively in smaller lakes. In some cases one species has ousted an earlier invader and the net result is just the puzzling web of closely related populations.

Since natural selection favours all sorts of ecological differences between sympatric populations, the ecological traits of the species are the last to disappear when introgression is in progress. This is the ultimate reason for the morphological likeness as opposed to ecological dissimilarity in whitefish, ciscos and some other groups of fish. This looks like an ecological split, or sympatric speciation.

Thus, after all, the puzzling whitefish and ciscoes are the result of an incomplete speciation according to wellknown principles. They are by no means exceptions to the rule of geographical isolation as a prerequisite for speciation but instead support this theory.

The Scandinavian populations of whitefish and ciscoes are built up by five whitefish sibling species and two cisco species. They have all rather similar ecological niches and they are partly able to change over from one "habitat" to another in the presence or absence of competing species. They will undoubtedly offer most interesting material for the study of competing species for a long time to come.

Many interesting problems have also been raised from the standpoint of animal geography and the study of dispersal. Scandinavia was deglaciated in recent times, the Baltic basin having been postglacially filled by an ice lake and the great Ancylus-lake with sea-stages in between. The dispersion of the various species, with their different tolerances to salinity, therefore becomes a complicated pattern.

2. Methods, material and acknowledgements

When my chromosomal studies of various salmonid fish species were terminated (SVÄRDSON 1945), the systematics of *Coregonus*-populations was studied from 1944 onwards. From the start two methods were regarded as being the most fruitful, and both were considered necessary for further progress.

First, experiments had to be performed in order to find out what characters were highly environmentally modified and thus of no use for studies of the systematics. At that time almost all characters so far used could be supposed, judging by the literature, to have excessive modificability. HILE (1938) had summarized the evidence indicating the environmental plasticity of the gill-rakers and practical experience had shown that growth, maturity and some morphometric relations could be very altered by a change of habitat or the density of the population in which the fish lived.

Transplantations from one lake to another were necessary and such operations which had been done with a practical purpose were sought out by searching in the literature and making use of the personal experience of the fishery officers. Time was spared when such experiments, which had already been carried out, could be studied in detail.

Further, cross fertilizations and selection experiments were planned and later successfully performed. Whitefish had been raised in aquaria (MELLEN 1923) but that was an exceptional case, and for the purpose of studying populations some other method had to be found. Fortunately, in the coniferous forests of northern Sweden there are numerous small tarns or lakes and in many cases whitefish fry had successfully been introduced in such small waters for practical purposes, in order to get fish for food. It was in fact known for centuries in Sweden that the growth of the fish could change considerably in such transplantations and, as no naturally laid roe survive in the small tarns (due to oxygen deficiency in winter), one single generation could be studied and the risk of contamination was small.

By this method of using small tarns as gigantic aquaria, it was possible to obtain numerous fish reared in cross- and selection experiments. Most of this field work was done by Mr. E. HALVARSSON, Fishery Assistent at the Kälarne Fishery Station in the Province of Jämtland. Mr. S. STENLUND, R. GYDEMO and H. PETERSON also assisted in some experiments, as did Mr. H. TOOTS in an experiment with selected parent fish.

The other main line of investigation was to collect whitefish material from as many natural populations as possible. Large samples were needed in order to make statistical treatments possible and samples from adjacent lakes were chosen to illustrate the process of subspeciation due to isolation or introgression.

Gradually the collecting of material was extended more and more. After some years of experiments it was found that gillrakers were of paramount importance and thus the collection could often be restricted to heads only. This in turn, of course, made still larger collections possible.

It was also gradually realized that whitefish from the whole country had to be studied, and the program was extended to cover the region from Lake Torneträsk in the far north to Lake Ringsjön in Scania and from the Baltic in the east to Lake Femunden in Norway in the west.

The great majority of fish was studied when preserved (in formalin). In some exceptional cases heads were preserved in salt, when collected in the field by Lapps or local fishermen.

In a few cases material from the museums has been studied. Professor H. RENDAHL in Stockholm and Prof. O. NYBELIN in Gothenburg were kind enough to lend some interesting samples of whitefish from Lake St. Skeppträsket, Lake Bullaren, Lake Ringsjön and River Ångermanälven. Most of the material in the museums, however, is too small, as a series of ten big fish is large for a museum, but small when population data is to be obtained. The majority of the samples investigated in these studies, when taken from nature, were very much larger, in some cases more than 1,000 fish.

Unpublished notes by the late Dr. TH. FREIDENFELT, who was a student of whitefish in Sweden and a pioneer in using statistical methods in taxonomical research, were kindly given me by a friend of FREIDENFELT, Lektor STEN ERIKSSON. Dr. ERIKSSON had carefully housed FREIDENFELT's material since 1937 and he generously handed it over to the Institute of Freshwater Research in 1956.

Dr. STEN VALLIN has kindly allowed me to include some unpublished notes about gillrakers of whitefish in the large Suorva-complex of regulated lakes. His material was taken in the 1920's and provides an interesting possibility for checking that no change has occurred since then.

Dr. E. DOTTRENS, in Geneva, was so very kind as to permit me to include in my tables the gillraker counts on the British populations of whitefish. This material was obtained by DOTTRENS from the British Museum and through fresh collections, and has so far not been published by DOTTRENS himself.

Dr. MAGNUS BERG, Tromsø Museum, Norway was very interested in my work and organized a collection by the Lapps of whitefish heads in the Kautokeino region.

Most of my studies have been concentrated on the gillrakers. It should, therefore, be mentioned that the gillrakers have been counted on the first left gillarch. The gillrakers on the other gillarches have been disregarded, since they are correlated to the number on the first arch. For the same reason, the study of the gillrakers was concentrated on the left side of the fish only. The length of the gillrakers was found to be of no use for taxonomic study. The length of the gillrakers is difficult to measure and it is also correlated to their number.

It should be specially stressed that all the gillrakers were included in the count, however small they were. Counting was always done in the laboratory, under a dissecting microscope. Counting in the field invariably gave too low figures and the method employed here gave a higher number of gillrakers than the method used by SMITT (1886). This was verified by counting some of his specimens, preserved in the State Museum of Natural History in Stockholm.

The time-consuming counting was done by technical assistants. My thanks are due to Mrs HELVE TOOTS, Mr. ALEX MÄÄR, Mr. GÖSTA MOLIN, Mr. EGON AHL, Mr. NILS-OLOV ÖSTERBERG, Mr. ARNE GAD, Mr. RICHARD ÖHMAN, Mr. ANDERS TÄGTSTRÖM, Mr. OLLE KEMPE, Mr. HANS-GUNNAR ANDERSSON and Mr. LEIF HILDEBY.

The collection of whitefish material in the field was accomplished in various ways by the local fishery officers, i.e. ARNE ANDERSSON, G. LÜNING, B. JOHANSSON, U. LUNDIN, J. WIDERBERG, J. E. JOHANSSON, E. A. SKOGLUND, L. STENBERG, G. SVENSSON, H. WIEDERBERG, H. FORSLIN, B. LUNDGREN, R. GYDEMO, K. B. JOHANSSON, E. MATTSON and U. LAPPEA, S. STENLUND and G. ÖQVIST. Dr. KARL MÜLLER also supplied whitefish from the Lule River.

My colleagues at the Freshwater Institute have in various ways given me very useful help, Miss MAJ STUBE fished for whitefish in an interesting locality in very hard winter weather, Mr. EGON AHL, RUDOLF SCHMUUL and ARNE GAD have made most valuable contributions.

Repeated grants from the Swedish Science Research Council enabled me to employ assistants for several years.

The writer is greatly indebted to all those who have facilitated his work in different ways.

3. The seven species and their nomenclature

Only vernacular names have so far been used in my papers on the Coregonid problem. The reason was that "the scientific names of the various whitefish species so far are most uncertain, due to the multitude of unsuitable descriptions and names of populations, the status of which is mainly unknown" (SVÄRDSON 1950).

The principles of nomenclature are based on orthodox species, which do no cross to form intermediate populations through introgression. Difficulties arise when these principles are applied to the network of *Coregonus*-populations, but in this chapter an approach will be made. It is realized, however, that it will take a long time before the nomenclature of the Coregonids has been stabilized.

First, the general situation of excessive introgression must be agreed on by the taxonomists concerned. Then all the proposed names must be listed and referred to their proper species. At present this cannot be done for all populations without some ambiguity owing to introgression.

When the situation has been further clarified, the International Commission on Zoological Nomenclature may be consulted and the present writer has had some preliminary contact with the Secretary of the Commission to obtain advice. At present the names used in this paper should be regarded as preliminary, only serving the ultimate purpose of being shorthand terms for reference.

The genus *Coregonus*

There has been a difference in opinion between European and American authors for some time regarding the delimitation of the genus *Coregonus*. The Americans, following KOELZ (1929) have split the genus into three different genera. The whitefishes were united into a restricted *Coregonus,* the ciscoes into *Leucichthys* and the round whitefishes were put into *Prosopium*. Recently, however, as can be seen from ESCHMAYER and BAILEY (1955) regarding *Prosopium* and WALTERS (1955) as regards *Leucichthys,* the trend has changed back to the European opinion and all these fish are united into *Coregonus*. *Stenodus,* however, is generally regarded as somewhat more remote and may, at least for the present, be left outside.

In Table 1 it is demonstrated that whitefishes and ciscoes may be artificially crossed and they may also produce an F_2-generation. The hatching of an F_2-generation has occurred in the spring of 1957 at the Research Station at Kälarne. The fry was vigorous.

There is no sterility barrier between the *lavaretus*-group (whitefishes) and the *albula*-group (ciscoes) of species. Spontaneous F_1-hybrids are found in nature, judging by circumstantial evidence from lakes with one population of ciscoes and only one known population of whitefish. The aberrant fish, however, could be mistaken for an occasional individual of a foreign whitefish population, introduced by man or belonging to an almost lost spontaneous population. The artificially produced hybrids between whitefish and cisco have the nose of the whitefish, making their identification when occurring spontaneously, troublesome.

The habitat of the ciscoes may also be inhabited by some of the whitefish species. This occurs principally when ciscoes are not living in the lake, as is the case in Sweden within a broad zone of lakes between the mountains and the highest shoreline of the Ancylus Lake. The whitefishes are much more pronounced wanderers and so they have distributed themselves in higher altitudes than the ciscoes have done.

As no major morphological difference exists, then the species may have the same ecological habits and, finally, as there is no sterility barrier between them, no important reason can be given in favour of splitting the whitefishes and ciscoes into different genera.

The writer has had no experience of the round whitefishes or *Prosopium*-species, but from published evidence it seems probable that they cannot be separated from the *Coregonus*-genus either.

This interesting fish genus thus comprises three groups of related species, each group being built up from a number of sibling, partly cryptic species. The groups are the *lavaretus,* the *albula* and the *cylindraceus* group of species. Only the Palearctic species of the first two groups are dealt with in this paper.

The *lavaretus*-group. Whitefishes

It seems as if all the hitherto known populations in the Palearctic could be comprised in only five different whitefish species. This is an opinion, based first on the rule that two sympatric populations must belong to different species and, secondly, on the principle that the genetic morphological character of the species is mainly the number of gillrakers.

If two populations A and B are distributed over the lakes in a region and in a certain smaller lake only one population occurs, which is fairly intermediate, this one is definitely not called a third species, C, but referred to as either A or B. If, on the other hand, the two species A and B are distributed over a region and there is a large lake with various ecological niches, in which lake there are also two populations neither resembling A, one resembling B but the final one very different from B (and still more different from A) this third population is tentatively regarded as a third species C.

The final decision as regards the species C is then withheld until more populations are found. No species concept is based on less than a group of different populations, having some elements of distribution in common. During the first years of my study the conservative figure of three different species was kept, then one was found to be in reality two and only after a further couple of years was the final fifth species regarded as certain.

The five whitefish species are:

C. pidschian (GMELIN). Described in Lin. Syst. Nat. ed. XIII. 1788.
C. nasus (PALLAS). Described in Pallas Reise, III. 1776.
C. lavaretus (LINNAEUS). Described in Syst. Nat. ed. X. 1758.
C. oxyrhynchus (LINNAEUS). Described in Syst. Nat. ed. X. 1758.
C. peled (GMELIN). Described in Lin. Syst. Nat. ed. XIII. 1788.

In no case could a species be identified morphologically from the original description but evidence from distribution, vernacular name etc. or later redescription made by an author counting gillrakers is in every case enough to permit the old, original names still to be used.

C. pidschian (GMELIN)

Gillrakers. The type locality is the River Ob in Siberia, where it is called "pidschian" by the Ostjaks. The Samoyeds call it "polcur". In the River Ob the species has 18—25 gillrakers, most often 22—23 according to BERG (1948). In the Bay of Gydansk between the Rivers Ob and Jenissei *pidschian* has only 17—23 gillrakers, with a mean of 19.8. This Bay is a better type locality, since *pidschian* probably through introgression with *nasus* has got a higher number of gillrakers in the River Ob.

Roughly 20 gillrakers seem to be characteristic for *pidschian* when it lives in a pure population. In Sweden the number is also around 20, and some populations have in fact a mean below 20. In Lake Constance the mean is again 20 in spite of probable introgression with species having higher numbers of gillrakers.

In Alaska the species, locally known as the hump-backed whitefish, has a range of 18—23 gillrakers, the mean being 20.7 (WALTERS 1955).

Ecology. The species is adapted to cold and survives only in Arctic environments or in lakes that are rather cold. It has a less varying growth rate than most of the other species. In the majority of known populations it is a large fish and often very old. It may continue to grow for 20 years or more. Pressed by other species (nasus) it may in exceptional cases be rather dwarfed, as in Lake Constance in central Europe, Lake Storlaisan in northern Sweden and in Lake Opeongo, Ontario (KENNEDY 1943), where this species is probably involved (see below).

It spawns in running water or at the shore in lakes, seldom in deep water. Its spawning period is from September—January, depending upon the cooling of the water (FABRICIUS 1950). The food is mostly bottom organisms, though plankton is taken to a lesser degree.

Distribution. JÄRVI (1943) thought this species was restricted to the Finnish drainages to the White Sea and then further eastwards. But its distribution is in fact much wider. In the Alpine region of Europe it occurs in Lake Constance and probably in some further lakes, in Sweden it is distributed over the southern highlands (Småland), which were first deglaciated and then suddenly isolated by the sea for a considerable period. It is also distributed in the uppermost parts of all large Swedish rivers, discharching into the Baltic Sea.

This species is fairly common along the Arctic border of Russia and Siberia and goes over to Alaska, where WALTERS (1955) recognised it as *pidschian,* though he followed BERG in ranking it as only a subspecies of *lavaretus,* which is impossible, in the light of the Swedish populations.

Over most of its range there is some introgression to its closest relative, the *nasus* species. Especially in northwestern America this seems to be true. How far *pidschian* is distributed into the range of *clupeaformis* is unknown, but in Lake Opeongo, Ontario, KENNEDY (1943) has described a case of advanced introgression between *clupeaformis* and a species having a lower number of gillrakers. This may most probably be *pidschian* and its local survival in Lake Opeongo a parallel to the recent discovery of *Coregonus coulteri* as a dwarfed population in Lake Superior (ESCHMAYER and BAILEY 1955).

Synonyms. In Lake Constance (cf. WAGLER 1937) this species is called *acronius,* SMITT (1886) called it *polcur* over parts of its range, PRAVDIN (1954) called it *lavaretus karelicus* and BERG (1948) *lavaretus pidschian.* In Alaska it was named *nelsoni* by BEAN (1884).

C. nasus (PALLAS)

Gillrakers. PALLAS named this species from the Bay of Ob but it also occurs in the River Ob, where it was called *schokur* by PALLAS. The gillrakers are 21—27 according to BERG (1948) and in the River Kara the variation is 21—24, in Lake Norilsk 21—27, mean 23.5, in the Bay of Gydansk the mean is said to be 22.0.

In the Ladoga and Onega region the mean is 23—24 in different populations, in the Swedish lakes Vättern and Vänern the species has a mean of 24—25 and in the Alpine region of Europe the mean is 23. Within the Baltic Sea introgression to *lavaretus* has occurred and locally the mean is as high as 27, but in pure populations (at Gotland) the mean is again 23—24. It is obvious, therefore, that *nasus* has slightly more gillrakers than *pidschian* but the difference between them is lessened by the fact that they often intergrade.

Ecology. The ecology of *nasus* is rather similar to that of *pidschian.* Like the latter it is a form adapted to cold, most often growing to be a large fish but its age may be somewhat less than that of *pidschian.* In several lakes in Sweden it has vernacular names allusive to its habit of going deep.

It is also known as deformed, through its gasbladder expanding when it is lifted up in gill-nets.

It spawns in running water or at the shore, in some cases fairly deep. Its spawning period is in the autumn, mostly October, but sometimes later, until December at least.

Its food is mostly bottom-organisms, plankton probably is of less importance.

Distribution. The *nasus* species has almost the same distribution as *pidschian* and the two species live sympatrically over most of their enormous range. *Nasus* lives in some populations in the Alpine region in Europe, i.e. sympatric with *pidschian* in Lake Constance. It also occurs in the old Litorina transgression area of northern Germany and Poland, in the Baltic Sea and it is a dominating species in the great Lakes Vättern, Vänern, Ladoga and Onega.

It is continuously distributed along the coast of the Arctic Ocean in Europe and Asia and ascends the great Russian rivers, where it is known as "tschir". It grows to be a very large fish in the rivers but also occurs in lakes, more or less as landlocked populations. When we come to the Bering Strait things are more complicated. WALTERS (1955) thinks *nasus* is distributed in some Pacific drainages, south to the Yukon River in the east and to the Bay of Korf in the west of the Bering Sea. How far it is spread into the Nearctic region depends on whether it is regarded as conspecific to *clupeaformis* or not.

Both *clupeaformis* and *nasus* have a somewhat higher number of gillrakers than *pidschian*. WALTERS lists several differences between *nasus* and *clupeaformis,* i.e. the length and shape of the maxillary, length and structure of the gillrakers, which are short and fairly smooth in *nasus,* long and spiny in *clupeaformis*. Finally the spawning season is said to be early summer for *nasus* but autumn for *clupeaformis.*

The difference in spawning seasons cannot be general, as BERG says *nasus* is an autumn spawner in Siberia, which is also the case in Europe. The nose is notoriously varied in whitefish and the Russian and most Swedish populations of *nasus* are not identical in this respect. The length of gillrakers is as a rule correlated to the number of rakers.

There is distributional evidence from postglacial spread in Scandinavia that *pidschian* is the older species here and that *nasus* first arrived during the Litorina period, i.e. the warm period of the Stone Age. If *nasus* came from the west, it must have crossed the Atlantic. If it came from the east, it spread from an Asiatic centre. As *pidschian* has passed the Bering Strait coming from the Palearctic invading the Nearctic, it is possible that *nasus* may have come from the Nearctic and spread in the opposite direction, into the Palearctic, thus first reaching its western fringe in Europe during a late postglacial time.

Though the Nearctic species of whitefish fall outside the scope of the present paper, it is suggested that *clupeaformis* and *nasus* are conspecific and that the introgression between *nasus* and *pidschian* in Alaska as well as along the Asiatic coast is responsible for the differences listed by WALTERS (cf. DYMOND 1943).

If so, *pidschian* and *nasus* are two closely related species, probably originating in Palearctic resp. Nearctic during the isolation of the last interglacial. During the last glaciation they could spread into the range of one another. This spread continued until postglacial times. *Pidschian* has been eliminated over most of the North American Continent, but its occurrence in Lake Opeongo, Ontario suggests a former distribution.

Synonyms. Within the Alpine region of Europe, *nasus* is known as *fera* (JURINE 1825). In northern Germany THIENEMANN (1915, 1922) called it *holsatus,* in Polish lakes KULMATYCKI (1927, 1928) named it *lavaretus polonica.* FREIDENFELT (1933) named it *amnipetens* in the River Gullspångsälven, Vänern. BERG (1948) called it *lavaretus* in the Baltic Sea, PRAVDIN (1954) identifies it as *baeri* and *ludoga* within the Carelian region of the U.S.S.R. Along the Russian Arctic coast it is called *nasus* but in the River Amur it seems to be conspecific to *chadary,* according to data in BERG (1948). In the Nearctic it is known as *clupeaformis.*

C. lavaretus (LINNAEUS)

Gillrakers. In Systema Naturae LINNAEUS refers to ARTEDI for this species. ARTEDI was born in Sweden at Anundsjö, on the River Mo, where whitefish from the Baltic Sea enters the river each autumn for spawning. He describes this river ascending population, which he also thought was spread along the whole Baltic coast of Sweden.

Unfortunately, there are two whitefish species in the Baltic (see Table 2). There can be no doubt, however, which one was referred to when the name of *lavaretus* was given. This was the dominant species, the one entering the rivers and having 30—31 gillrakers as a mean. This number has been decreased in comparatively recent times, as it is the result of introgression between a species having 23—25 gillrakers (*nasus*) and a second one, having 33—34 gillrakers. This latter species must be the true *lavaretus,* conforming to the original description. It occurs at present in its purest form in the southeastern part of the Baltic Sea, along the East Prussian and Baltic coasts, where it has 33—34 gillrakers, and where *nasus* with its low number of 23—25 lives sympatrically.

Along the Swedish coast most populations are intermediate, but there is a marked tendency for more gillrakers (30—31) in populations ascending the rivers, and a lower number (25—27) in those populations, spawning deeper in the outer skerries. This duality in the whitefish along the Swedish coast reflects the present stage of introgression between *lavaretus* and *nasus.*

Upstream in the rivers, in numerous lakes, *lavaretus* again has its normal number, i.e. around 32—34.

Lavaretus has the same number in the Alpine region of Europe, i.e. in lake Constance and in a British lake. It was for a time quite a mystery why *lavaretus* should be confined to the Baltic region. BERG (1948) and most other Russian authors had no information regarding *lavaretus,* except for listing *pidschian* as a subspecies of *lavaretus*. But there is indeed no reason whatsoever for such an opinion.

Finally, the significance of dwarfing in this species, when living sympatrically with other species in the lakes of Sweden, was realized. It is often strongly dwarfed, 10—20 cm, and lives pelagically as a cisco, though it may still be a wanderer and spawn in running water. When some specimens of *C. tugun* from Jenissei were inspected at the Museum of Natural History in Stockholm it was quite evident that *tugun* was no cisco but a dwarfed whitefish, just as *lavaretus* was often known to be.

The gillraker number in *tugun* is, according to BERG, 27—33 more often 28—29, which is the same number that *lavaretus* has in Sweden when intergraded to *nasus*.

Ecology. As said above, the ecological plasticity is typical for this species. When it lives in large lakes (Ladoga, Onega, Vänern) it can coexist with *nasus* without being dwarfed but in the smaller lakes, especially the colder ones in the higher altitudes, *lavaretus* looks more and more like a cisco. The nose is very much shortened in these small fish, but they never have pronounced antrose premaxillaries, as the true ciscoes have. *Lavaretus* is often a decided wanderer, both in the Baltic Sea where marked fish have recently moved 400—500 kilometres, as well as in the small lakes where it often ascends the tributaries for spawning. In some cases, however, it may also spawn by the shore. In Siberia, the *tugun* is also known as a river-living fish.

It should be added that the dwarfs occur in cold lakes, when *lavaretus* lives there beside some other species. In some cold lakes, however, it is the only species of its genus and then it is large. This suggests that the dwarfing process is not principally due to temperature but to competition.

Distribution. Palearctic region, from central Europe and the British Isles in the west to the Bering Strait in the east. BERG says that *tugun* is distributed from Ob to Chatanga but *lavaretus* seems also to be conspecific to *C. ussuriensis* in Amur. Not known from the Nearctic.

Synonyms. In the Alpine region it is known as *wartmanni* (BLOCH 1783). In the Litorina transgression area of northern Germany it is known as *maraena* (BLOCH 1779). In the British Isles it is called powan or *C. clupeoides* (REGAN 1908). In Sweden it has been named *microcephalus* and *microps* by SMITT (1886) and GÜNTHER described quite a number of forms from Lake Vänern, all being *lavaretus, nasus* or their intergrades. All GÜN-

THER's names are, therefore, invalid, PRAVDIN (1954) calls it *lavaretus mediospinatus* in Lake Ladoga and *lavaretus lavaretoides* or *lavaretus olonensis* or proposes still other names for it in Carelia. In all the Carelian lakes some introgression seems to have occurred and the definite decision whether a certain population should be referred to *lavaretus* or *nasus* is difficult or impossible from published evidence only. In the drainages to the White Sea PRAVDIN calls it *lavaretus arnoldi.* Then it disappears (probably only due to insufficient information) reappearing as *tugun* in the River Ob. The most eastern population seems to be *ussuriensis.*

C. oxyrhynchus (LINNAEUS)

Gillrakers. It was convincingly demonstrated by REDEKE (1934) that the name *oxyrhynchus* was given by LINNAEUS to a whitefish population, living in the Rhine and adjacent coastal waters. REDEKE found the gillrakers of the recent population to be 36—44 with a mean of 40.0. Like the description of *lavaretus,* the *oxyrhynchus* was also based on a fairly introgressed population of the species concerned. It is true that a whitefish species having 40 gillrakers is spread over many lakes in western Europe, but it is uncommon for it to be living in running water, still more uncommon for it also to be found in the sea and, finally, for it to have a long nose!

The long nose no doubt came from *nasus* which still has its long nose in isolated populations, i.e. in Lake Vänern and Lake Vättern. But in other recent western populations the long nose has survived in *lavaretus* in the southeastern Baltic (the Germans called it Schnäpel) and in *oxyrhynchus* in the Rhine. The change-over of the genes for a long nose must be due to introgression, and not, as has been suggested, to convergent evolution, i.e. the long nose should have a triple, independent origin.

The gillrakers of *oxyrhynchus* are 40 in number all over western Europe, though some slight variation occurs due to introgression with other species. The gillrakers are roughly 40 in the "Edelmaräne" of northern Germany, and in the Peipus population. On the Arctic coast it is known as *autumnalis* from the River Mesen to the River Kolyma and has 40—42 gillrakers as a mean (BERG 1948). The same is true of the American populations which were listed by WALTERS.

Ecology. This species is related to *lavaretus* and resembles it in being ecologically plastic. It may be large and fast-growing as in Lake Hjälmaren and Lake Peipus, but when living sympatrically to other species it is very often dwarfed. Those populations have very short noses, just like dwarfs of *lavaretus,* and may be confused with ciscoes, in the habitat of which they occur. The group of species "between" whitefish and ciscoes known from Russia seems to be in fact only dwarfed whitefish. As the Russian system was based on morphological criteria only, the very deviating phenotypic characters of the dwarfed populations set them strangely aside from the rest.

Oxyrhynchus is not river-running as often as *lavaretus*. In Lake Peipus Mansfeld (1930) could demonstrate that it fed on fish but normally it takes plankton. It has difficulties in coexisting with *lavaretus* and usually one of the *pidschian-nasus*-pair lives together with one member of the *lavaretus-oxyrhynchus*-pair, much more seldom all four can coexist in one lake, as in Lake Constance and Lake Storsjön. Over most of their range in Sweden *lavaretus* ousts *oxyrhynchus*, just as *nasus* ousts *pidschian*.

Oxyrhynchus is the species most tolerant to warm water of all the whitefishes known. It has thus survived in many shallow lakes in western Europe, which are too warm for the other whitefish.

Distribution. This species is very widely spread. It lives from the British Isles in the west over the whole of Europe and along the Russian and Siberian coast and lakes, in Lake Baikal (called *migratorius*) and on the Alaskan side of the Bering Strait. WALTERS gives its distribution in the Arctic Ocean drainages from the White Sea eastward to Bathurst Inlet in Canada, in the Pacific Ocean drainages south to the Alaska Peninsula in the east and the River Penzhina in the west.

As it is found in most of the lakes which were early free from ice in the deglaciation of central Europe and in Swedish lakes situated the highest, it must have lived at the border of the ice during the Wisconsin-Weichsel glaciation. *Lavaretus,* on the other hand, ousts *oxyrhynchus* from its lakes but does not occur in the earliest isolated lakes. Thus *lavaretus* must be a late invader, just as *nasus*. Though both are Palearctic and *oxyrhynchus* is distributed in the western Nearctic as well, *lavaretus* probably arrived in the Baltic region from the east during a late stage of the deglaciation or post-glacial time.

Synonyms. Within the Alpine region this species is known as *macrophtalmus* (NÜSSLIN 1882), in northern Germany and Poland it was called *generosus* by PETERS (1874). In Lough Neagh, Ireland THOMPSON (1835) named it *pollan,* in Haweswater and Ullswater it is identified as *clupeoides stigmaticus* (REGAN 1908) and in Lake Bala it was called *clupeoides pennanti* by the same author. In Lake Ringsjön, Sweden, it was named *nilssonii* by VALENCIENNES (1848) and the well-known population in Lake Peipus was identified as *lavaretus maraenoides* by PRAVDIN (1931). The populations in Ladoga and Onega PRAVDIN (1954) calls *lavaretus pallasi.* WIDEGREN (1863) named it *megalops* in Lake Storsjön, Jämtland, in middle Sweden. In Russia or in Siberia it is known as "omul" or *autumnalis, omul, lepechini* or *migratorius* (BERG 1948), in Alaska it was earlier called *laurettae* (WALTERS 1955).

C. peled (GMELIN)

Gillrakers. GMELIN referred to LEPECHIN, who had seen the species at Pustozersk, situated in the lower River Petschora. This is the type locality. BERG (1948) gives the number of gillrakers as 49—68 for *peled* and 44—65 for *muksun,* which is regarded as conspecific by the present writer. This is the highest number of gillrakers in any whitefish. In the Finnish lakes this species has a mean of 50 gillrakers (JÄRVI 1928—1953) and in the few Scandinavian lakes the species has 45—50 rakers on an average, though there are scattered populations having a somewhat lower number probably due to earlier introgression.

Ecology. This species may wander in the great rivers flowing into the Arctic Ocean, where it grows large. But it also occurs in landlocked populations which are much more stunted and in some cases fairly dwarfed, judging from the evidence presented by BERG and PRAVDIN. The main reason why *peled* is united with *muksun* by the present writer is that they have the same number of gillrakers, furthermore *muksun* is said to go in the rivers but *peled* lives in the lakes. No proof of sympatric living has been found in the Russian literature by the writer.

It is closer to the *lavaretus-oxyrhynchus* pair than to the *pidschian-nasus* pair. This is evident not only from the gillrakers but also from the ecology, which may be rather plastic. In the northern Swedish Lake Uddjaur-Storavan in the Skellefte River this species is large and spawns in the streams but in Lake Storuman, in the Ume River system further south, the species is dwarfed, living pelagically and spawning rather deep in December at the shore. This plasticity is a further argument for the Russian scientists having been mistaken, when they split the species into two according to the phenotypical appearance of populations living in various lakes and the sea.

Distribution. *Peled* has the most restricted distribution of the whitefishes in the Palearctic. It is not known from the New World, either as *muksun* or *peled,* but BERG lists the same distribution for both — River Mesen or Kara in the west to River Kolyma in the east. But there is no doubt that it also lives in Carelia, in the lakes in central Finland and finally in the uppermost lakes of the Swedish rivers. An isolated population in Denmark with 45 gillrakers may belong to *peled,* which certainly has been ousted by the later invaders over parts of its range in Europe.

Synonyms. The large-sized populations going to the Arctic Ocean are called *muksun* by the Russian authors. It has also been named *cyprinoides, pelet, wimba,* according to the synonyms listed by BERG. PRAVDIN (1954) calls it *lavaretus multispinatus* in Carelia. The Danish population was referred to *generosus* by OTTERSTRØM (1922). The Swedish ones in Lapland were called *aspius* by SMITT (1886) after the local vernacular name of "asp". They were degraded to being only a subspecies of *lavaretus* by BERG. It must be stressed that BERG has used the name *lavaretus* in a very peculiar way. Though he was extremely open to morphological (but less to ecological) differences between the Russian or Siberian whitefishes, he did not hesitate to group all the whitefish in western Europe into one great species, the *lavaretus.* This means that in the greater lakes, i.e. Lake Constance, Lake Siljan, Lake Storsjön and Lake Hornavan three or four different "forms" of *lavaretus* should coexist, according to BERG, having different morphology and strikingly different ecology too. The populations have been separated into "sorts" by the fishermen from time immemorial. It was stressed as early as by WIDEGREN (1863) that coexisting populations with clear-cut morphological and ecological characters must be termed species.

The *albula*-group. Ciscoes

The American name for these fish is adopted here, since it seems very convenient for the whole group of species, which is most diversified in North America. In this paper only the Palearctic species are discussed.

BERG recognizes two species in this group, the present writer also thinks there are two species, but they are not the same as BERG's.

As when delimiting *lavaretus* BERG also restricted the *albula* by its distribution geographically. He thinks *albula* and *sardinella* are two allopatric species. The borderline between them, geographically, lies in northwestern Russia. *Albula* still occurs on the Kola Peninsula, but *sardinella* lives in the White Sea, in the lakes in the Solotesky-Isles, in Kolgujev and in Petschora. No ecological difference is found. The morphological difference is extremely slight; the distance from nose to dorsal fin is said to be more than 42 % of the total length in *albula,* less in *sardinella.* If so, *sardinella* is also found in some Swedish lakes.

Characteristic for the ciscoes, morphologically speaking, is the protruding lower jaw, which is always marked, ecologically it is their restricted niche of pelagical life, their feeding on plankton, their growing only moderately large and appearing in running water only accidentally, i.e. when a lake is flooding.

The two cisco species recognized by the present writer are:

C. albula (LINNAEUS). Described in Syst. Nat. ed. X 1758.

C. baunti, MUCHOMEDIJAROV. Described in Dokl. na pervoj nautjnoj sessii Jakut. bazy AN SSSR, 1948, according to BERG (1949, III, p. 1323). The original description has not been seen, the journal is unknown in Swedish libraries.

The reason for splitting the ciscoes into two different species is ecological, as they have had the capacity of living sympatrically within small lakes for thousands of years. In three different Swedish lakes, which belong to different rivers, populations of ciscoes deviating from *albula* live beside normal *albula.* The deviating populations all spawn in late April or during the first days of May, while *albula* always spawns in autumn or early winter.

In searching for evidence of other surviving populations of this spring-spawning species of cisco, it was found that some ecologically deviating populations have been named, but only *C. sardinella baunti,* named by MUCHOMEDIJAROV in 1948 from the River Zipikan, tributary to the River Vitim in Siberia, was clearly a population which also spawns in spring. MUCHOMEDIJAROV states, according to BERG, that the spawning occurs from medio April to the first days of May. In 1942, May 5th, the major part of them were spent.

For this reason *baunti* has been used here as the specific name for this sibling cisco species. When more information is available, it may turn out to be an incorrect name owing to priority.

Introgression between the *albula* and the *baunti* may be part of the explanation for the deepwater forms of cisco, described as *lucinensis* from northern Germany, *ladogensis* in Lake Ladoga, and *kiletz* in Lake Onega. It may also be part of the explanation for the two waves of spawning ciscoes, reported from the Rivers Kar and Kolyma by BERG. As far as the present writer has found, no evidence of real spring-spawning has been produced for any one of all these ecologically somewhat deviating populations of ciscoes. *Baunti* may therefore have priority, though it was proposed rather recently.

C. albula (LINNAEUS)

Gillrakers. BERG says *albula* has 36—52 gillrakers and *sardinella* 34—52. The known variation from Russian populations is thus 34—52. From nearly three thousand specimens investigated from Swedish localities the variation 37—55 is found, but local populations have means from 39.9 to 47.8. The highest number of gillrakers is found in the innermost parts of the Gulf of Finland, where the variation is 48—58, according to JÄRVI (1942) and the mean as high as 52.0.

Ecology. The common cisco is less plastic than some of the whitefish species. It may grow large in recently established populations (artificially introduced) which expand with the rich supply of food. It may also be severely stunted and spawn as a fish, less than 10 cm in length. But it is always a pelagic plankton-feeder and goes in running waters only when driven out by flooding in the lakes. In such exceptional cases they have also been found moving upstream.

Distribution. *Albula* has a very wide distribution. It is known from some lakes in the British Isles (where it is called vendace), it lives in many lakes of northern Germany and Poland (but not in the Alpine region), also in Scandinavia, Russia, Siberia, according to WALTERS it even occurs in the New World. He gives its distribution as being from Bathurst Inlet in Canada and, in the Pacific Ocean drainages, to the Yukon River. As WALTERS had said *albula* (locally known as *sardinella*) and *artedi* may be conspecific. The present writer thinks this is very probable indeed and, if so, the *albula* may be the most widespread of all the Coregonine fishes.

Synonyms. In the British Isles *albula* has been called *vandesius* and *vandesius gracilior* (REGAN 1908). Otherwise the species has not been given as many names in Europe as the whitefishes have. Local deep-water forms have been cited above, none was argued as being an independent species. Within the White Sea range *albula* has been called *merkii* and *sardinella* (BERG 1948 for references) and on the Nearctic side of Bering Strait it was named *pusillus,* though DYMOND (1943) showed this to be a synonym for *sardinella.* It is the opinion of the present writer that *albula* is also conspecific to *artedi,* which may add a number of new synonyms to the list.

C. baunti, MUCHOMEDIJAROV

Gillrakers. MUCHOMEDIJAROV found the population described as having 32—38 gillrakers, usually 36—37. This seems to be a lower number than the *albula* has. This is an interesting possibility but at present it must be judged with caution, the fish investigated by MUCHOMEDIJAROV being stunted and this having possibly given them a lower number, just as a small one-summer-old whitefish has not yet got its final number of gillrakers.

In the Swedish populations the number of gillrakers is the same as in the coexisting *albula* population, i.e. about 42 as a mean. But this can, of course, be secondarily due to introgression and part of the geographical variation in the *albula*-populations can in fact be caused by past introgression between *albula* and *baunti.*

Other morphological characters were found by RUNNSTRÖM (1940) but these are known or supposed to be environmentally induced by warm water.

Ecology. At present no further difference between *albula* and *baunti* is known other than the spring spawning period of *baunti,* as opposed to the autumn spawning of *albula.* When fishing for *baunti* in Lake Ören in late April of 1957, we found it spawning very deep, 20—30 metres, which may be a further difference.

Distribution. At present this species is only known from the paper by MUCHOMEDIJAROV, who gives its distribution as lakes belonging to the River Zipikan in Siberia, and in addition from three Swedish lakes. These are Lake St. Holsjön, Lake Åsunden and Lake Ören. The lakes lie within different water systems, but all the populations could have invaded their present homes from the Baltic Ice Lake, 10,000 years ago. The species certainly lived in this great ice lake, sympatrically to *albula,* which indicates that the distribution of the species may be large. The gap between the Swedish and the Siberian localities is probably not real. It is also possible that *baunti* has been ousted by *albula* from parts of a great area of distribution.

Synonyms. None. MUCHOMEDIJAROV called it a subspecies of *sardinella.*

4. Experiments on the environmental modification of the phenotype

Growth and morphology

When a number of sibling fish species is to be studied, even the small differences in phenotypical appearance are important. The study of whitefishes is, however, much complicated by the fact that the fish have an advanced capacity for being modified by environment. They are plastic in ecological habits and, as a consequence, in a number of morphological characters, which have been used in the taxonomy.

It has been known for a long time that when dwarfed whitefish are transplanted into lakes, where there were no whitefish before, the dwarfs undergo a tremendous change in their growth and may become quite large. If they can spawn in their new environment their progeny may grow still bigger. As taxonomists have used allometric characters for their diagnoses, a dwarfed whitefish species transplanted into a new environment may grow out of its old diagnosis to fit into another one (SVÄRDSON 1949).

This well-known observation, based on multitudes of transplantations done by the fishermen in northern Scandinavia for hundreds of years, has been verified by scientists in recent times (OLOFSSON 1934, RUNNSTRÖM 1944, SVÄRDSON 1950).

MARTIN (1949) found inflections in allometric growth occurring at certain periods during fish development. Thus fish of an identical total length may have different measurements for their body parts, if they have, since the fry stage, grown at different speeds. In a controlled experiment of whitefish transplantation, parents and their progeny grew rather differently and they had, at the same total length, different sizes of eyes and heads, furthermore different anal heights, body heights and snouts, all of which have been used as stable characters in the taxonomy (SVÄRDSON 1950).

It was also found that the number of scales along the side of the body could be strongly modified by the temperature in which the fry developed after hatching. In one case young whitefish, one-summer-old and raised in a pond, had a mean of 85.7 scales while their parent population, spawning in a river discharging into the Baltic Sea, had a mean of 97.0 scales. In a number of other cases, transplanted populations also changed their number of scales (SVÄRDSON 1952).

The spawning period

The spawning period has ecological significance as part of the isolation barrier between species of whitefish, coexisting in the same lake. It has also some morphological consequences because of the temperature sensitivity of developing fry. Fishermen often recognize a "sort" of whitefish by its spawning habits.

The proximate stimuli, releasing the spawning in whitefish were described by FABRICIUS (1950). A case of early spawning in an autumn with exceptionally cold weather was reported by SVÄRDSON (1953). The proximate stimuli, however, must have been moulded by natural selection, acting through the ultimate factor, i.e. the survival of the fry the next spring.

In an earlier paper (SVÄRDSON 1951) it was described how a whitefish, spawning in October at the shore of the Baltic Sea, was transplanted during the 1940's into some lakes in the Parish of Malå. Spontaneous whitefish in those lakes, which were thought to have died out, had always spawned in late December. The fishermen were immensely surprised by the new "sort" spawning in October, obviously following its proximate stimuli, to which photoperiodicity must probably be added.

The first generation of Bure whitefish in the Malå lakes was a great success. It was released in the lakes as newly hatched fry. When these introduced fish spawned in the lakes, however, the fry must have perished, as there has been a very disappointing renewal of the new population. The old indigenous forms, which were thought to have disappeared, have, on the other hand, been restored by some good year-classes.

The explanation, thought the most probable at present, suggests that the introduced single generation of Bure whitefish succeeded in predating the perch to lower numbers. Thus the old whitefish species got a chance of having rich year-classes. But the introduced species had proximate stimuli, resulting in a spawning period which deviated from that of the indigenous populations, and was consequently probably of low survival value. Therefore, the introduced whitefish species reduced the perch by its predation on perch fry but was incapable of propagating itself abundantly. Natural selection must gain immense strength in such a case towards changing the spawning period to higher fitness.

There are some cases known in which an introduced whitefish population has changed its spawning period in one or two decades. The details are not very well known, but there is circumstantial evidence that some changes are due to natural selection, some to the proximate factors (e.g. late spawning in a spring-fed lake).

Gillrakers

NÜSSLIN (1882) started the practice of counting gillrakers in whitefish. This has later grown to be the standard method in demonstrating a difference between two populations. In an earlier paper (SVÄRDSON 1952) I have summarized the evidence for the number of gillrakers being genetically determined and for this character being the *only one* hitherto used in whitefish taxonomy, which is known to be environmentally stable. The phenotype is, as regards gillrakers, equivalent to the genotype.

In this chapter the present evidence will again be reviewed and discussed in relation to the tables.

Gillrakers do not change with time. There are samples of whitefish from the Lakes Luoktanjarkajaure and Alemusjaure, within the Lule River system, from 1928 and the 1950's. No change in gillraker number has occurred. Dr. FREIDENFELT sampled several lakes within the Klarälven River system in the 1920's and 1930's. Samples taken again during the present investigations indicate no change.

A sample from Lake Stora Skeppträsket, preserved at the Museum of Gothenburg, was taken in 1913 and has the same average as recent samples. The same is true of samples from Lake Ringsjön, Lake Bullaren und River Ångermanälven, compared with recent ones, though here the different collections were made 70—80 years apart. Finally, Lake Mälaren was separated from the Baltic Sea during the twelfth century (GRANLUND 1930) due to the upwarping in postglacial times and its whitefish population has still just the same average as that outside Lake Mälaren, in the skerries of the Stockholm Archipelago.

Gillrakers do not change in transplanted populations. The evidence from a number of transplantations was summarized earlier (SVÄRDSON 1952). In some cases a slight change seemed to have occurred, but later research has stressed the possibility that stray hybrids or specimens of unknown indigenous populations may have appeared as sources of variety and error.

In Table 1 some cases are given in detail. The whitefish in Lake Dellen was transplanted to Lake Öjungen in 1918. Recent samples from both lakes indicate no change.

Fry from the population spawning in the mouth of River Indalsälven was raised in a pond at Kälarne and fry was in another year also released in Lake Kölsjön, (River Dalälven), in which there was no whitefish previously. No change in the number of gillrakers could be demonstrated.

The three whitefish species from Lake Idsjön, within the Ljungan River system, have been intensively studied for a decade (cf. SVÄRDSON 1953, 1954). In Table 1 some transplanted populations of one Idsjö-species, taken with no selection, again display no changed number of gillrakers.

Gillrakers change in response to selection. In the autumn of 1950 individual selection of extreme fish was made at the spawning place of the most common species in Lake Idsjön. These selected fish were allowed to be parents to a progeny, which should have a lower or higher number of gillrakers than the mother population, if the extreme gills of their parents were based on their genotype.

The progeny of the fish with 32 gillrakers had a mean of 33.8, while the progeny of the fish with high numbers had 39.0 and 38.3 as mean values.

Thus the selection indicated a polygenic inheritance of the number of gillrakers (Table 1).

Gillrakers are intermediate in hybrids. Five different experiments with artificial fertilization of eggs of one whitefish by sperm from another species are reported in detail in Table 1. In all cases the F_1-hybrids are intermediate and thus indicate a polygenic mechanism behind the number of gillrakers.

One of the experiments includes hybrids between whitefish and cisco, i.e. between members of the *lavaretus* and the *albula* group of species. As pointed out in a previous chapter a second generation of hybrids was produced in the spring of 1957. Their gillrakers cannot be counted until the autumn of 1957.

The hybrids between the whitefish of Lake Brunträsket and that of Lake Stora Skeppträsket were fertile and a second generation was sampled and included in Table 1. The lower number in the F_2-fish, as compared with the F_1-ones may be due to unconscious selection at the artificial fertilization. The fish were raised in small tarns distributed in the vast coniferous forests, and fertilization could not be done except during a few days in the autumn, when the females were ripe. This usually happened when the tarn was frozen and the ice not strong enough to bear a man but certainly too strong to permit a boat to be used!

A further detail of Table 1 is the repeated observation that one-summer-old fish, about 10—12 cm in total length, regularly give a slightly lower number of gillrakers than the same population when sampled later on. The close coincidence between subsequent samples from the same population may also be especially emphasized.

5. The Scandinavian populations

The firm basis for an understanding of the sibling whitefish species and their complicated pattern of introgression must be a thorough knowledge of the actual populations. It is of little importance at present to give data on growth, allometric or meristic data, as these rather reflect the environment in which the fish live, than the populations themselves. Consequently, the available data on the gillrakers have been gathered and are given in a number of Tables. In some cases, where introgression is going on or sympatric species are of different size, length data (in millimetres) have been included in the Swedish material.

The Baltic Sea.

The material is given in Tables 2 a and 2 b. The southeastern shore of the Baltic is frequented by two clearly different whitefish populations, *lavaretus* with 33 gillrakers as a mean and *nasus,* with 23—25. The sample from the Hela Peninsula has a rather low number, 20.3 as a mean, but this sample is probably not equivalent to the others. The count, of course, may give deviating number if the smallest, lateral rakers are not included. At present the Hela-sample cannot be regarded as certain, which should indicate *C. pidschian.* If it should be verified by new investigations, the local survival of *pidschian* as a relic may be discussed.

The species *oxyrhynchus,* with 40 gillrakers, has been found in the Baltic Sea as some expelled specimens off the River Neva and the River Narva, or, finally, off the River Salis, coming from Lake Burtneck (MANSFELD 1930). There is nothing to indicate that *oxyrhynchus* spawns in the Baltic Sea. This species, therefore, in contrast to what THIENEMANN (1953) thought, does not belong to the Baltic whitefishes, which are only two in number: *lavaretus* and *nasus.*

Introgression between *lavaretus* and *nasus* is of no significance in the southeastern part of the Baltic Sea, but along the Swedish Coast (except for Gotland) as well as the Finnish Coast, the introgression is a fact. It may in some cases lead to quite intermediate populations, having 27—28—29 gillrakers as a mean, but in the greater rivers, the bimodality of the whitefish is often obvious. In those cases one species (*lavaretus*) ascends the rivers to spawn, while the other species (*nasus*) spawns at the outermost skerries of the archipelago. At the mouth of the River Indalsälven the *lavaretus* has 31 gillrakers and *nasus* 27, at the mouth of Kemi and Torne Rivers *lavaretus* has 29—30 and *nasus* 25—26. The duality of the whitefish has always been known and commented on by the local fishermen.

Lavaretus, with more gillrakers, is no doubt the most common of the two along the Swedish Coast, and as it is the only one ascending the rivers, it is certain that this was the species to which LINNAEUS attached the name of *lavaretus,* when he referred to ARTEDI's earlier description of it.

In Table 22 the Swedish samples of ciscoes are listed. The common cisco, *C. albula* lives according to JÄRVI (1942) in brackish water where the salinity is less than 2 ‰ at the surface and less than 3 ‰ in the bottom layers. This means that *albula* is isolated in the northernmost part of the Gulf of Bothnia, where it has 44—47 gillrakers as a mean, and it lives as another isolated population in the innermost parts of the Gulf of Finland, where it has an average of 52 gillrakers (JÄRVI 1942). The two isolated populations no doubt have mutual genetical differences.

The Torne River system

The material is given in Table 3. This drainage system is characterized by few rapids and waterfalls and the whitefishes have had an easy task in spreading upstream.

Lavaretus and *nasus* are the dominant species. In Lake Idijärvi *lavaretus* is rather pure (mean 33.4) and in the Norwegian lakes Stuorrajavre and Gåskinjavre *nasus* is also rather pure (24.8 and 24.9) but in a number of other lakes introgression between them is evident. In Lake Märtäjärvi (mean 30.2) the *lavaretus*-genes are quite dominant but in the great Lake Torneträsk (mean 27.3) *nasus* is more dominant, judging by the gillrakers. The ecology of the fish harmonizes with that.

Pidschian has been mainly ousted by later invaders but survives locally, i.e. in Lake Sautusjärvi (mean 18.5). *Oxyrhynchus* is also largely eliminated, but survives in the Torne River at Jukkasjärvi, where it lives as a dwarfed population (mean 37.8) and as an introgressed population in Lake Nakerijärvi.

The Kalix River system

The material is given in Table 3. This river is also comparatively free from rapids and waterfalls.

Lavaretus and *nasus* are again dominant species. *Lavaretus* is only slightly introgressed in Lake Vettasjärvi (mean 31.2) and is a dwarfed population in Lake Pauki (31.5). *Nasus* is probably rather pure in Lake Kaalasjärvi (mean 24.9) but introgressed in Lake Saivo (26.6) in which lake fry from the Råne River has also been released. The replacement process, in which *nasus* ousts *pidschian* by means of swamping is in full swing in several lakes. In Lake Paittasjärvi the mean is 23.1, in Lake Akkajärvi the gillrakers of the introgressed population are as low as 22.1 and there are obvious signs of the same development in Lake Tjautjasjärvi. *Oxyrhynchus* has survived in Lake Paittasjärvi as a dwarfed population (mean 38.6) and there are small-sized populations in Lakes Tjautjasjärvi and Akkajärvi, which belong to this species or are possibly strongly introgressed remnants of *peled*. This cannot be judged with any certainty at present.

The Råne River system

The material is given in Table 4. At the mouth a population spawns which ascends from the Baltic (29.4). Fry from this population has been commercially hatched in large quantities and released in various lakes in northernmost Sweden. A population of *pidschian* (19.8) has survived in Lake Degervattnet.

The Pite River system

The material is given in Table 4. *Lavaretus* is by far the most dominant species in this river. Populations, which may be pure, are found in Lake Tjeggelvas (32.9), Lake Skärfajaure (33.6) and Lake Malmesjaure (33.0), which are the largest lakes within the river system. These *lavaretus* populations are large-sized fish. In smaller lakes as well, i.e. in Lake Sleng, the *lavaretus* lives in a pure state (34.0). *Nasus* has influenced the low average of the population at the mouth (26.6) but otherwise as the stray fish have low numbers, for example in Lake Suddesjaure, they are probably *pidschian.*

The Åby River system

The only population studied in this river is the one in Lake Lauker (22.1), which is probably an introgressed *pidschian.*

The Byske River system

The material is given in Table 4. Two lakes, i.e. Gråträsket and Långträsket have been sampled. Both contain flourishing populations of *pidschian* (both means below 20) and a coexisting population of dwarfed whitefish, in which *lavaretus* is certainly represented. In Lake Långträsket (35.0) some genes from *oxyrhynchus* may be included in the actual stock. As seen from Table 22 the cisco, *C. albula,* was sampled in Lake Gråträsket.

The Lule River system

The material available is included in Table 5. The main river has some remarkable waterfalls and it is very strange that *lavaretus* is the only species living in the uppermost lakes, which are nowadays united by artificial regulation to one single, great lake, the Akka. All samples from various parts of this great water reservoir have about 31 gillrakers. It is tempting to suggest that man has helped the wandering *lavaretus* across the waterfalls at some earlier unknown time. It may here be added that the common practice of releasing live fish in lakes, known to be uninhabited by fish before, is proved to have taken place in the twelfth century in Norway by HUITFELT-KAAS (1924) and as pointed out by HUITFELT-KAAS and EKMAN (1910), this practice is so simple that it may have been discovered by man at any cultural stage.

In the Lakes Kårtjejaure, Langas and St. Lulejaure the *oxyrhynchus* (or *peled*?) species has probably been living and it is still found in Lake St. Lulejaure, but is very introgressed and more or less swamped by *lavaretus* in Lake Kårtjejaure. In very recent times, great annual quantities of newly hatched fry from the Råne River (29.4) have been released in Lake St. Lulejaure and, as seen from the Table, this population has been established.

The main Lule River gets an important tributary from the south, called the Lilla Lule. In this river the whitefishes are more in conformation with the general scheme, and this, of course, strengthens the view that man has changed the populations of the main river. In the Lilla Lule all the lakes are inhabited by whitefish with few rakers. These dominating populations are mainly *nasus,* but in some places as in Lake Peuraure, Lake Karats and Lake Saggat, the means are so low that *pidschian* is probably involved as well.

In Lake Saggat there lives a certain population of *peled* (50.4) and downstream, in Lake Skalka (48.5), there is another population of the species and, finally, in Lake Randijaure *peled* is probably introgressed to the other species, as there is almost every number between 20 and 53 represented in the samples from this lake. In Lake Vaikijaure a *lavaretus*-population (31.7) is dwarfed, while the sympatric *nasus* (24.5) is a large-sized fish.

The Skellefte River system

The material is given in Table 6. This river is not as easily accessible as the systems situated more northerly.

Lavaretus is distributed over the whole system and lives as a pronounced dwarfed population in the upper great lakes. It is most dwarfed in Lake Hornavan, where it lives sympatrically to *oxyrhynchus* (which is also dwarfed) less so in Lake Uddjaur and Lake Storavan. In some of the smaller lakes, i.e. Lake Kokträsk, Lake Vågträsk, Lake Bockträsk and Lake Malåträsk it is a large-sized fish.

Nasus is not found with certainty in the river system. There is one population of whitefish in Lake Brunträsket with 23.9 gillrakers, but as the neighbouring lakes are inhabited by *pidschian* and OLOFSSON (unpublished) found two species in Lake Brunträsket in the late 1920's, one with a low, the other with a higher number of gillrakers, introgression of *pidschian* by *lavaretus* may be involved. In the 1940's when fry from the Bure River was introduced into Lake Brunträsket (SVÄRDSON 1951), there was only one indigenous population left in the lake, i.e. the one with 23.9 gillrakers as a mean.

Pidschian is represented in the river system with large-sized and economically important populations in the great Lakes Hornavan, Uddjaur and Storavan. It was further sampled in Lake Jutis (19.9), Lake Lajnijaur (18.8), close to Lake Brunträsket, and Lake L. Skeppträsket (20.6).

Oxyrhynchus is widespread and lives in Lake Jutis (37.5), in Lake Hornavan as a deep-water form (!) introgressed to *lavaretus,* in Lake Ö. Verbosjön (40.0), in Lake St. Skeppträsket (39.9), and in Lake Kvammarn (37.3) probably again introgressed to *lavaretus.*

Peled has survived in the three great lakes. In Lake Uddjaur (45.3) and in Lake Storavan (45.7) it is fairly pure but in Lake Hornavan it is known to hybridize with *pidschian.* This is shown in Table 6, where it is found that in Lake Hornavan fish in the size group 251—350 have rakers between 16—51. Most of the fish with numbers above 25 are probably hybrid fish. In the smaller lakes *peled* has disappeared, no doubt due to competition and swamping by the other species.

Albula was sampled in Lake Järvträsket (Table 22). It has an extremely low mean number of gillrakers (41.0), which has its only equivalent in the population from Lake Gråträsket belonging to the Byske River system (39.9).

The Bure River system

Included in Table 6 is a sample from the mouth of the short Bure River. The whitefish ascending the river to spawn is an introgressed population of *lavaretus,* having 28.4 gillrakers. Fry from this population has been commercially spread over many lakes (Svärdson 1951). In the lakes of Malå Parish (Lake Brunträsket, Lake Lajnijaur) the new "sort" spawned in October, two months earlier than the indigenous forms, and displayed poor powers of survival, except for the introduced generations.

The Ume River system

The material is given in Table 7. As judged from the recent ascent of salmon, this river has been easily available for whitefish species.

Lavaretus has a very peculiar distribution in this river. It lives in Lake Gautsträsk (32.6) and Lake Gertsträsk (31.1) which are both lakes in the uppermost part of some small tributaries, i.e. they are "toplakes". Since man is proved to have introduced whitefish in other lakes within the river system in recent times, the exceptional "upstream" occurrence of *lavaretus* is doubtful. Again *lavaretus* is represented in the heavily introgressed population that moves in the lower part of the river with 27—28 gillrakers or less.

Nasus and *pidschian* form a pattern of introgression and replacement within the whole river system. In Lake Storlaisan two populations of rather small-sized fish have 20.6 and 23.2 gillrakers. In Lake Storvindeln *pidschian* is rather small, ascending a tributary for spawning (20.4), while *nasus* (22.9) is a large fish, spawning on skerries in the lake. Again, in the third branch of the river system, in Lake Storuman, the bimodality of the population is reflected by the cline 22.3—23.8—25.8 from the northernmost part of the lake downwards to the river, just downstream from the lake. In some smaller lakes i.e. Lake Sikträsket (25.8) and Lake Falträsket (23.1) the process is probably finished and *nasus* is the only one left. Whitefish has been introduced by man in the 1920's to Lake N. Björkvattnet and upstreams (26.2). Formerly only char and trout lived there.

Peled lives in Lake Storlaisan (46.9) and in Lake Storuman (43.9), in both cases as a dwarfed fish. The dwarfed population in Lake Storvindeln (39.5) may be a heavily introgressed *peled*. *Oxyrhynchus* is not found with certainty within the river system.

The Ångermanälven River system.

The material is given in Table 8. This river is steep and has a number of rapids and waterfalls. It belongs to the region of Scandinavia that has had the most marked postglacial upwarping. The sequence of invading whitefish species can, therefore, be studied very well in this river.

Lavaretus is not represented in the uppermost parts of the River Vojmån until Lake Volgsjön. In the River Fjällsjöälven it inhabits Lake Nappsjön and spawning fish from this lake were transported to Lake St. Arksjön, where there was then, 1928, no whitefish (OLOFSSON 1934). In the third branch of the great river system, the River Faxälven, whitefish was introduced into Lake Görvikssjön in the 1850's (EKMAN 1910) and NYSTRÖM (1863) reports that it spread downstream to Lake Russfjärden and the whole of Ströms Vattudal. The present domination of *lavaretus* in the River Faxälven is therefore not natural. The population ascending from the Baltic into the mouth of the River Ångermanälven has 30.6 gillrakers and is an introgressed *lavaretus*.

Nasus has a most doubtful occurrence in the river system. There are some populations with 23—24 gillrakers i.e. in the Lake Dikasjön and the northernmost part of the great Lake Vojmsjön but this is an introgressed *pidschian* everywhere. The only population, where genuine *nasus* may be a fact is the one in Lake Flåsjön (24.6).

Pidschian is an important species in Lake Skikkisjaure, (19.6), Lake Dikasjön (24.7), northern Lake Vojmsjön (22.9), southern Lake Vojmsjön (21.0), Lake Malgomaj (21.6) and Lake Volgsjön (22.4). It is the largest whitefish in the lake everywhere. In the lower parts of the river system, especially where *lavaretus* comes in, *pidschian* has disappeared. The three specimens in Lake Mårdsjön (19.7) may be the last remnants of a former population.

Oxyrhynchus lives in the topmost lake, Skikkisjaure (37.2), and also in Lake Dikasjön and northern Lake Vojmsjön. This last population is extremely dwarfed and was discovered by Dr. FABRICIUS in the 1940's. The fish were found in the stomachs of trout and were ripe, being three years old when ten centimetres long. In Lake Malgomaj another dwarfed population occurs (37.8), as well as introgressed populations in Lake Ormsjön (36.7) and Lake Tåsjön. In Lake Russfjärden, where *lavaretus* was introduced, the indigenous *oxyrhynchus* has been almost swamped. The smaller fish, less than 251 mm, have 35.5 gillrakers, while the larger fish have 32—33. In one river mouth whitefish spawns in October and again in December. The advanced introgression of *oxyrhynchus* by *lavaretus* has been achieved since the 1850's.

Peled lives in a population of medium-sized fish in Lake Vojmsjön, with 45—46 gillrakers as a mean. In Lake Dikasjön which runs into Lake Vojmsjön, *peled* and *oxyrhynchus* have hybridized intensively and formed an intermediate population. After a recent regulation of the level of Lake Vojmsjön, *peled* has again invaded Lake Dikasjön as can be seen in Table 8, where the samples (Dikasjön) from 1951 are compared with those from the year 1955.

Peled has been ousted from the other lakes, but some genes seem to survive in Lake Tåsjön.

Finally, *Coregonus albula* was also sampled within the Ångermanälven River system (Table 22). The actual locality, Lake Sörsjön, is below the level of the highest shores and the *albula*-population has a low mean number of gillrakers (42.5).

The Indalsälven River system

The material is given in Table 9. There are several steep waterfalls in the lower part of the main river, but the highest shores are far inland.

Lavaretus is distributed in the main river from the mouth (31.3) up to Lake Storsjön and Lake Nälden. Samples have been taken during the spawning period for three years in the tributary to Lake Nälden (River Nästån) (Tables 9 a—c). In these Tables the spawning period of *lavaretus* can be seen to overlap that of *nasus* in a rather regular manner. In the River Hårkan *lavaretus* has spread up to Lake Hotagen, where it is strongly dwarfed, and in the River Långan the same is true as regards Lake Landösjön. In the uppermost lake of the Hårkan, Lake Valsjön, *lavaretus* does not occur, nor has it spread to Lake Näckten near Lake Storsjön. It is doubtful if the population in the uppermost lake, Öjarn, in the River Ammerån (34.2), is indigenous. The species has been introduced by man in other lakes in the close vicinity, running into River Ångermanälven. The same is true of Lake Häggsjön (31.0).

Nasus lives in the artificial lakes within the main river, in Lake Hammarforsmagasinet (25.2) as well as Lake Midskogsmagasinet (25.7). It also lives in the Gesunden (25.7) as a large-sized fish, while the sympatric *lavaretus* is dwarfed (30.1). The *nasus* species has been introduced by man in this century to Lake Kallsjön, Lake Sällsjön, Lake Yttre Oldsjön, Lake Rönnösjön and Lake Landösjön. The fry was probably taken in all cases from Lake Liten or Lake Ockesjön. *Nasus* has partly ousted *pidschian* and the replacement process can be illustrated by Lake Ockesjön (25.2) as compared to the population in the River Dammån, debouching into Lake Ockesjön (21.0). In the rapid Kvitsleström there are two channels for the water, and two whitefish spawning grounds. In one locality the spawning fish have 24.3, in the other 22.1. *Pidschian* still survives, though introgressed, in Lake Näckten (21.3) and Lake Nälden (21.4) and, in a purer state, in the lakes within the River Ammerån. In Lake Ottsjön the sampled population had a mean of 19.3, in Lake Gåxsjön 19.9, while in Lake Hammerdalssjön the *pidschian* is fairly introgressed.

Oxyrhynchus is widespread. It lives beside *nasus* in Lake Helgesjön, but all the whitefish in this "toplake" were introduced by man since the 1850's when it was a char lake. In Lake Storsjön *oxyrhynchus* is less dwarfed than *lavaretus,* in Lake Näckten it is a small fish, as in Lakes Ottsjön and Gåxsjön. But in Lake Valsjön and all the subsequent lakes of the River Hårkan, the *oxyrhynchus*-populations consist of large-sized fish.

The introgression of *lavaretus* and *oxyrhynchus* in the River Hårkan is extremely interesting. *Oxyrhynchus* (large) is by itself in Lake Valsjön, *lavaretus* (large) is on its own in Lake Häggsjön. Both live, in Lake Hotagen, *oxyrhynchus* as a large fish, *lavaretus* as a dwarf. The same is true in the next lake, Lövsjön, but here introgression has gone so far that the means are almost the same, 37.1 and 35.1. We are here faced with two sympatric populations, one of large fish, one of dwarfs with different spawning periods and places but almost the same number of gillrakers. In the next lake, downstream, *nasus* has complicated the pattern still more. We have two populations, again one dwarfed with 28.8 gillrakers and one of large fish with rakers from 22—40, the mean of which is 28.5. If viewed apart from the general pattern of introgression, the River Hårkan whitefishes would be completely incomprehensible.

Peled is unknown in the whole of the Indalsälven River. *Albula* may occur in the lower regions but was not sampled.

The Ljungan River system

The material is given in Table 10. The Ljungan, Indalsälven and Ångermanälven are probably the three rivers, in which the whitefish have had the most difficulty in spreading upstream. All have waterfalls and rapids and all lie within the region of highest upwarping during the postglacial time.

Lavaretus is not a dominant species, though it occurs from the mouth (31.0) upstream to Lake Holmsjön in the main river and Lake Röringen (34.5), Lake Bodsjön (31.0) and Lake Pån (33.0) in the Gimån River. It may have been recently introduced by man in the Gimån River, as the replacement process in which *lavaretus* ousts *oxyrhynchus* has not proceeded very far. In Lake Ansjön the introgression is evident. There is a larger whitefish (33.7) spawning at the shore and a smaller whitefish spawning later and somewhat deeper (36.3). The latter is *oxyrhynchus,* which is probably being eliminated.

Oxyrhynchus is a more dominant species within the river system. There are many populations with 35—40 gillrakers as a mean and these are probably all slightly introgressed *oxyrhynchus.* They are as a rule small fish, some of them real dwarfs. In Lake Skåsjön (37.4) the population is on its own in the lake, as far as known, but it is dwarfed all the same.

Two lakes are especially interesting, both as "toplakes" in their drainage areas. The first is Lake Locknesjön (41.5) where the variation 37—48, though slight introgression to *pidschian* in the lake, indicates a rather high gillraker number for the old spontaneous population. It may, in fact, be *peled* or at least *oxyrhynchus* introgressed by *peled*. The other lake is Lake Öfsjön, in which size-grouping of the spawners (Table 10) clearly indicates bimodality of the population, as do the growth rates as well. There are two extremes of growth rates with a number of intermediates in between, a very protracted spawning period and scattered spawning grounds. This is, of course, a sign of the very last stages of an advanced introgression between two forms. Now, the smallest fish have 41 gillrakers, the larger 39.5, though the peak frequences are 42 and 38 respectively. It seems very tempting to explain this as an introgression between *peled* and *oxyrhynchus*.

Otherwise, no certain *peled* population is found in the Ljungan River system.

Pidschian survives in several lakes. In the main river it lives in Lake Storsjön (20.9), in Lake Holmsjön (20.5) and Lake Navarn (21.6) and probably in all the lakes between them. In the Gimån River *pidschian* lives in Lake Locknesjön (21.8), in Lake Bodsjön (20.6), in Lake Sundsjön (22.4), in Lake Idsjön (20.4) and in Lake Sicksjön (22.9). In all these lakes *pidschian* is a large-sized fish, and grows very old.

Nasus is of doubtful occurrence. In Lake Idsjön a dwarfed population has 25.9 gillrakers, as found in samples from several years totalling 1.461 specimens! As described earlier (SVÄRDSON 1953) two other populations are living sympatrically, *pidschian* with 20.4 gillrakers and a river-spawning medium-sized fish with 36.0 (sampled in more than 800 specimens due to population studies). The river-spawning species has more gillrakers than a normal *lavaretus,* though the habit of wandering in streams for spawning is typical for *lavaretus*. The population with 25.9 gillrakers on the other hand is dwarfed, which has never been proved for *nasus* elsewhere. Since this would be the only population of *nasus* in the river, if accepted, the alternative interpretation seems somewhat more probable, i.e. that *lavaretus* has obtained the low number of 25.9 rakers through introgression, *oxyrhynchus* being the river-spawning population. Introgression into *oxyrhynchus* by *lavaretus* may have lowered its gillraker number and strengthened the ecological habit of river-spawning.

A small sample of *albula* from Lake Holmsjön has a high mean (47.5). Cf. Table 22.

The Delångersån River system

The material is included in Table 11. In Lake Dellen there lives a probable *nasus*-population (23.5) and in Lake Hångstaörn an *oxyrhynchus*-population (37.5) was sampled.

The Ljusnan River system

The material is given in Table 11. The Ljusnan River was probably rather easily invaded by the whitefish species in their postglacial spread.

Lavaretus and *nasus* are the dominant species and they intergrade abundantly. In Lake Vikarsjön live two whitefish species, one large (*nasus*) with 26.6 rakers and one dwarfed (*lavaretus)* with 34.1. Somewhat more upstream, in the great Lake Lossnen the introgression has gone somewhat further, *nasus* is once more a large fish with 28.7 and *lavaretus* on the other hand a dwarf with 32.0. The gap has thus been partly filled. There is a cline from Lake Lossnen up to Lake Ö. Vattnan at the top of the river, illustrated by the means 28.8—28.6—26.9—23.1. This probably represents the amount of introgression by *lavaretus*. The Öjungen population was introduced from Lake Dellen, (cf. Table 1) that in Lake Orrmosjön (23.6) is probably genuine.

There is no certain population of *pidschian* or *peled* left in the river. *Oxyrhynchus* survives in Lake Orrmosjön (39.2 and 40.8). The bimodality of the smaller fish in this lake may be due to some remaining *peled*-genes. The populations in Lake Målingen and Lake Öjingen (35.7 and 36.4) are introduced fish from Lake Idsjön in the Ljungan River. The heterogenous population of Lake Tandsjön (tributary of River Voxnan) is a hybrid one. *Nasus* from Lake Dellen (23.5) and *lavaretus* from Lake Siljan (33.8) were introduced in Tandsjön in the last decades. They began to hybridize immediately.

The Dalälven River system

The material is given in Table 12. The Dalälven River has been easily accessible for whitefish.

Lavaretus and *nasus* are the dominant species. In Lake Siljan *lavaretus* was known as "ryssing", as early as in a document written in 1440, and spawning-places which are still used were then said to be known for a long time (GRANLUND 1955, p. 77). *Lavaretus* (33.8) is introgressed by *nasus* (27.3) in Lake Siljan and the balance between these two species varies in different parts of the Dalälven River. At the mouth *lavaretus* (30.8)-genes are probably responsible for the wandering habit.

Pidschian survives in Lake Siljan on at least one spawning-ground, at Alderäng (21.6). Elsewhere it is mainly ousted, though genes from *pidschian* are still recombining in the whitefish of Lake Idresjön and Lake Särnasjön.

Oxyrhynchus is rare. In the isolated Lake Amungen it is the only species (38.2) and in Lake Horrmundsjön (38.1) it has been introduced from Lake Tisjön in the Klarälven River system. In Lake Venjan, however, it is certainly indigenous, but nowadays heavily hybridized to *lavaretus* (36.9 and 33.2 respectively). *Oxyrhynchus* is the more dwarfed population in Lake Venjan.

Peled is unknown in the Dalälven River system.

Albula lives in several lakes, as parts of the drainage area were flooded in postglacial times by the Ancylus Lake. It has been sampled from three lakes (Table 22).

The Norrström River system

The material is given in Table 13. *Lavaretus* was sampled in Lake Mälaren (31.1) and in Lake S. Hörken (30.0) while *oxyrhynchus* (40.6) lives in Lake Hjälmaren. Both are large fish. *Albula* lives in several lakes (Table 24), it is of economic importance in Lake Mälaren (SVÄRDSON 1956).

The Motalaström River system

The material is given in Table 13. This drainage area was deglaciated very early and could be populated by whitefish living in the Baltic Ice Lake, before this lake was replaced by the first period of the Baltic Sea. The water level was suddenly lowered about 40 metres, when the border of the glaciers retreated north to the mountain Billingen and passage was free to the Atlantic.

Lavaretus and *nasus* have both invaded the river system. *Lavaretus* lives in Lake Ylen (34.5), Lake Unden (32.3) and Lake Kyrksjön (35.8) while *nasus*, with a very long snout indeed, lives in Lake Vättern (25.1). The *nasus* in Lake Unden is short-nosed (25.1). More interesting, however, is the occurrence of *pidschian* in Lake Ören (20.9), in Lake Sommen (21.2) and Lake Drögen (21.4). This last population has been transplanted to Lake Narven, as has the sympatrically introgressed *lavaretus*-population of Lake Drögen. Apart from the long-nosed *nasus* in Lake Vättern, a second species (24.2) also occurs. This seems to be a marked introgressed *pidschian*-population. Neither of the two is dwarfed. The occurrence of *pidschian* in Lake Vättern is strengthened by the fact that SMITT (1886) in his *Tabulae metricae* reports "vitsikar" with 16—18 gillrakers. Some change may have occurred since SMITT's days. He also found some stray "grönsikar" with 31—35 rakers. This *lavaretus*-population has escaped notice in the present investigations, or has probably disappeared from Lake Vättern.

Oxyrhynchus lives in Lake Nätaren (38.1), while the population in Lake Mossjön (39.8) was introduced by man from an unknown locality. The large-sized whitefish of Lake Åländern (42.9) may be a *peled*. A number of lakes within the river system are inhabited by the common cisco, *C. albula*. As seen from Table 22, Lake Ören is one of the three lakes in which the second cisco species, the spring-spawning *baunti* is known to live sympatrically to *albula*.

If *peled* is preliminarily accepted as the probable species in Lake Åländern, we are faced with the interesting fact that the Motalaström River system, though it is a small one, is inhabited by all the seven *Coregonus*-species of the Palearctic region. This is due to the fact that some deep and cold lakes are situated in an area, which was exposed to invaders from the Baltic Ice Lake. New whitefish species have experienced profound difficulty in entering the river system ever since the Yoldia-time.

The Emån River system

The material is included in Table 13. *Lavaretus* was sampled in Lake Fagerhultssjön (34.4) while *nasus* was sampled in Lake Vallsjön (25.9). The population of Lake Assjön (29.9) was introduced by man, probably from Lake Mien (vide infra).

The Alsterån River system

The sample from Lake Alstern (39.3) is an *oxyrhynchus*-population. It is included in Table 13.

The Mie River system

The sample from Lake Mien (29.3) is most probably an introgressed *lavaretus*. It is included in Table 13.

The Mörrumsån River system

In Lake Åsnen there lives a whitefish (35.9) which is rather intermediate between *lavaretus* and *oxyrhynchus*. *Albula* (Table 22) lives sympatrically and the two species have been artificially crossed and the hybrids raised (Table 1).

The Skräbeån River system

Finally in Table 13 is also included a sample from Lake Immeln (35.4). It cannot be determined at present, if this should be mainly referred to *lavaretus* or *oxyrhynchus*.

The Rönne River system

The material is given in Table 14. The whitefish in Lake Ringsjön has not changed its number of gillrakers since the 1880's. It is an *oxyrhynchus*-population (37.5), which lives in this warm lake. Professor SVEN NILSSON brought some specimens to VALENCIENNES, who named it *nilssonii*. It has been known in Scandinavia under that name ever since.

The Lagan River system

The material is given in Table 14. This river system is dominated by *oxyrhynchus*. It lives in Lake Övringen (37.0), Lake Algunnen (36.7), Lake Rusken (39.0), Lake Flåren (38.3), and Lake Vidöstern (39.7), while *lavaretus* has spread upwards to Lake Bolmen (33.9). The second species of Lake Allgunnen (27.5) is difficult to identify, preliminarily it may be called mainly *lavaretus*. But representatives of the two cold-water whitefishes have also lived in the system. In Lake Hindsen, which is known as a spring-fed cold lake, there is a surviving population with 23.4 gillrakers. It is probably *nasus*.

The Nissan River system

Whitefish live in Lake Stengårdshultsjön (28.4). It may be an introgressed population of *lavaretus*. It is doubtful if the population is spontaneous.

The Ätran River system

The material is given in Table 14. *Lavaretus* lives in Lake Såken (32.3) while the population of Lake Yttre Hallången (29.5) is known to have been introduced by man. Probably the fry came from Lake Mien, known to be the source of many plantings. In Lake Visen the whitefish belongs to the *oxyrhynchus* species (38.0), while *pidschian* has survived in Lake Sämsjön (20.9) and Lake Fegen (19.9). The whitefish of Lake Åsunden is of doubtful origin, only three specimens are known so far. *Albula* lives in several lakes and *baunti* is found in Lake Åsunden (Table 22). The drainage system of the Ätran River served as part of the outlet of the Baltic Ice Lake. The general parallel distribution of *pidschian* and *baunti* is significant.

The Viskan River system

The material is given in Table 14. *Lavaretus* with 34.3 gillrakers lives in Lake Tolken (Ås härad) but the species also lives in another Lake Tolken (Marks härad) where it has 28.4 gillrakers, probably through introgression. It may have been introduced here (from Mien?). *Nasus* may be the species in Lake Ärtingen and Lake Öresjön but *pidschian* is certainly the species in Lake St. Holsjön (18.6). It is again significant that *albula* and *baunti* live sympatrically in Lake St. Holsjön, which is the third lake in Scandinavia where this is known to occur.

The Götaälv-Klarälven River system

The material is given in Table 15. The Klarälven River comes from Lake Femunden in Norway, flows through the Swedish Province of Värmland

and debouches into the great Lake Vänern. Some other rivers also run out into Lake Vänern and its waters finally flow through the River Göta down to the Kattegat.

Nasus was sampled in the archipelago off the river and there is also a population spawning in the Göta River (24.1). *Nasus* and *lavaretus* are the only whitefish species (apart from the cisco) spawning in the great Lake Vänern. They are both large-sized, *lavaretus* is probably more dominant in the north, where samples from Hammarö are rather pure (33.6). *Nasus,* on the other hand, spawns around Kållandsö where it has a very long nose, a light pigmentation pattern and 25.4 gillrakers in some samples. In the Åråsviken Bay there is an ascending river-spawning population (24.7), which was named *amnipetens* by Freidenfelt.

By the western shore of Lake Vänern, at Mellerud, intermediate populations occur (31.5) and there is not the slightest doubt that *lavaretus* and *nasus* intergrade in Lake Vänern. But the introgression has not proceeded as far as in the northern parts of the Baltic Sea and all the fishermen are convinced that there are two species (at least). The *nasus* is known, apart from its long nose, for its habit of going into the depths. It expands its gas-bladder when lifted up in a net by the fishermen.

Nasus is also known from some smaller, northern lakes within the system. It lives in Lake Yngen (24.6), in Lake Värmeln (23.8) and as an introgressed, winter-spawning deep water population in Lake Femunden in Norway (about 27—28 gillrakers). *Lavaretus* has also spread over the whole system, and was sampled in many lakes.

Oxyrhynchus has survived in some places. It lives in Lake Skagern (36.9), in Lake Lelången (37.5), in Lake Öjesjön (39.5) (both probably introduced by man), Lake Stora Gla (39.4), Lake Storjangen (38.0), Lake Knon (37.2), and as a strongly introgressed population in Lake Femunden.

Most interesting to note, *peled* lives in Lake Femunden (about 44 gillrakers) and also in Lake Fryken (43.0). *Pidschian* is unknown. *Albula* lives in many lakes (Table 22).

Huitfelt-Kaas (1924) suggested that the whitefish in Lake Femunden reached the lake by invasion from the Swedish River Dalälven, i.e. from its western branch. Huitfelt-Kaas thought the rapids of the Klarälven River were too strong hindrances for whitefish. There is a series of Norwegian lakes by means of which invasion to Lake Femunden could have occurred from the Dalälven River. This is an interesting possibility. If true, it means that *peled* has been ousted from the Dalälven River and *pidschian,* which lives in Dalälven River, has been ousted from the Klarälven River. Though this is possible, the fact, that the eel has been capable after the building of the Trollhättan canal in the 1860's, of ascending to Lake Vänern and through the Klarälven River almost up to Lake Femunden (Huitfelt-Kaas, op. cit.), indicates that the hindrances to fish passage upstream in the Klarälven River may be less severe even to whitefish than HUITFELT-KAAS supposed.

The Kyrkälven River system

The material is given in Table 14. Lake Södra Kornsjön and Lake Bullaren are both inhabited by rather pure *lavaretus*-populations (34.0 resp. 32.9). The population of Lake Bullaren has not changed its gillraker number since 1873.

The Randselva River system

Included in Table 14 are some of the counts performed by Mr. K. ENGE, who has been so kind as to allow me to cite from his unpublished paper on the whitefishes of Lake Randsfjorden in Norway. There are three distinct populations, with different growth rates and partly different numbers of gillrakers. The *strømsik* has 35.6 gillrakers and may best be classed as a *lavaretus*-population, which may have been introgressed slightly by an *oxyrhynchus*-population that is now gone. Secondly there is the deep water form, called *vintersik* or *djupvannsik*. The habit of going in the depth indicates that it is an introgressed *nasus* (29.6). Finally comes the *grunnsik,* which is ecologically an equivalent of the *strømsik,* but with the gillrakers of the *vintersik* (29.8). As *strømsik* and *grunnsik* are living in both ends of the long lake, they may in fact be conspecific. The different number of their gillrakers may be due to different amounts of introgression to the *nasus,* the bulk of which spawns near the *grunnsik*. A similar case of different amount of introgression in both ends of a great lake is known from the Lake Vojmsjön (Table 8).

The interesting case of Lake Randsfjorden may be tentatively explained, at present, as a rather complicated introgression pattern between *lavaretus* and *nasus*. An *oxyrhynchus*-population has probably previously inhabited Lake Randsfjorden but has been eliminated.

6. Some previously described whitefish populations

The Finnish whitefish populations

The new material from Sweden and Norway which has been presented in Tables 1—15 and Table 22 may be compared with the old data, brought to light by earlier students of the whitefish speciation problem.

In order to faciliate such a comparison a number of tables have been prepared, in which some populations described by earlier authors are summarized. The purpose has not been to give a complete summary but only to give a general impression of how the populations vary according to the very same principles that have been discussed for the Scandinavian populations. The species involved are also identical.

In Table 16 data are given about the gillrakers of Finnish whitefish populations in the rivers which discharge into the Baltic or Lake Ladoga.

Within the Kemi River system all populations seem to be *lavaretus* or *lavaretus*-populations introgressed by *oxyrhynchus*. Some of them, i.e. in Lake Latvajärvi, are more or less pure *oxyrhynchus*. Lake Paatinkii on the other hand is inhabited by a *lavaretus*, which is probably introgressed by *nasus* (28.8).

The Kumo River system is inhabited by *peled*, which was sampled in all three lakes. Their gillrakers are very numerous (means 48.5—49.2).

The Kymmene River is inhabited by *oxyrhynchus*, which may in some cases be slightly introgressed by *lavaretus* (i.e. Lake Lievestuore). The Saima-Vuoksen River is inhabited by *oxyrhynchus* and *peled*.

Albula is known to be abundant in Finland.

It is a strange fact that *pidschian* and pure *nasus* do not occur in Finnish river systems discharging into the Baltic Sea or Lake Ladoga. It is also rather impressive that *lavaretus* is not nearly as dominant as *oxyrhynchus*. *Peled* has survived better than in Sweden.

When we come to those Finnish rivers, which discharge eastwards to the White Sea or the Arctic Ocean (Table 17), the picture is very different.

Within the Paatsjoki River, all the lakes have a strong *nasus*- or *pidschian*-component in their whitefish populations. In Lake Inari *pidschian* and *lavaretus* seem to live sympatrically. In the Kovda River *pidschian* is frequently found, though *lavaretus* and *oxyrhynchus* also occur. In the Kem River *pidschian* is again represented, though Lake Kirpistö is inhabited by a population, in which *lavaretus* may have been introgressed.

Professor JÄRVI, who has devoted so much interest and effort to the study of the Finnish whitefish populations, observed the difference between the populations of the east-flowing and west-discharging rivers. He remarks (JÄRVI 1943, p. 34) that the difference "wird in Zukunft vielleicht weniger scharf hervortreten" but so far this has not happened. Since *pidschian* has reached the Baltic Sea basin and invaded a number of Swedish rivers, the reason cannot be that the species is of extreme eastern origin thus living only in those parts of Finland, exposed to the Arctic Ocean, as suggested by JÄRVI as a possibility.

The populations of the Carelian and adjacent regions of the U.S.S.R.

In Table 18 some gillraker counts from PRAVDIN's papers have been summarized. They have all been made in the northwestern part of the U.S.S.R.

In Lake Ladoga both *nasus* and *lavaretus* occur (cf. Table 2), though PRAVDIN has not published the detailed figures of his *lavaretus*-samples (which he calls *mediospinatus*). The *lavaretus*-populations of Lake Onega are better represented in Table 18. They are somewhat different in various parts of the great lake, no doubt due to different amount of introgression by *nasus*. The *lavaretus-nasus*-balance is very much the same in the three great Lakes Vänern, Ladoga and Onega, in which both species dominate.

In the smaller Carelian lakes *pidschian* also appears, i.e. in Lake Pjal and Lake Sjam. In Lake Sjam *peled* lives sympatrically to *pidschian,* which reminds us of the same thing in some Swedish lakes which are remote and were isolated rather early (i.e. Lake Vojmsjön). *Oxyrhynchus* lives in the Neva River, in the Vukosen River and in Lake Peipus and the Narva River. In the smaller Carelian lakes *oxyrhynchus* has only been sampled in Lake Pert (37.8), but it has perhaps been overlooked owing to being dwarfed.

Thus the whitefish populations of the Lake District of the U.S.S.R., which have been most intensively studied so far in Russia, are of the same categories as the Scandinavian populations and there is no reason whatsoever to introduce other specific names for them.

The Danish populations

In Table 19 the material published by OTTERSTRØM (1923) has been rearranged. It is striking that *pidschian* and *nasus* are not found, while the cline in gillrakers found by OTTERSTRØM to be parallel to a salinity gradient is due to introgression of *lavaretus* by *oxyrhynchus* upstream. Some populations, like that of Lake Glenstrup (46.4) may best be classed as *peled*. This is important, as it again indicates that *peled* was one of the three whitefish species (*pidschian, oxyrhynchus, peled*) living at the border of the glaciers, or in the Baltic Ice Lake.

The British populations

Through the courtesy of Dr. E. DOTTRENS of Geneva, it has been possible for me to include data, which he obtained on the British populations (Table 20), and which have been very little known.

Lavaretus is the species living in Loch Lomond (33.9), while all the other populations must be referred to *oxyrhynchus*. If the higher number of gillrakers in the population of Lough Erne is due to introgression by *peled,* or, alternatively, the others are introgressed by *lavaretus* cannot be judged at present.

The Alpine populations

The whitefish populations in the Alpine region have been most thoroughly studied for a long time. In Table 21 the data in WAGLER (1937) have been rearranged. Again, it must be stressed that the Table is not a complete summary, some counts by STEINMANN, DOTTRENS and others have been omitted. However, the populations, which are omitted, are easily fitted into the scheme.

Pidschian lives in Lake Constance and in Lake Thun. *Nasus* has invaded the region and survives (called *fera*) in Lake Constance and Lake Chiemsee and is introgressed to *lavaretus* in a number of cases. *Lavaretus* lives in several lakes, mostly introgressed to *oxyrhynchus* which is the really dominant species. It is doubtful whether *peled* has ever lived in the region. *Albula* does not occur in the Alps but only in northern Germany and Poland.

7. Summary

1. The speciation in the whitefish group has proceded along the same lines as in other vertebrates. Sympatric speciation has not occurred. The species evolved during geographical isolation have later, when they could spread during the last glacial period, come to live sympatrically over vast areas of the Palearctic region.

2. The genus *Coregonus* is discussed. Seven species are redescribed for the Palearctic region. They comprise five whitefishes: *pidschian, nasus, lavaretus, oxyrhynchus* and *peled* and two ciscoes: *albula* and *baunti*.

3. Experiments on the phenotypical variation of whitefishes are described. The capacity for environmental modification is profound in these fish. Only the number of gillrakers is so far proved to be genetically based. Several species were artificially crossed and their F_1-hybrids have been proved to be fertile. The possibility of introgression in nature is thus experimentally established.

4. The whitefish and cisco populations of a great many Swedish lakes and localities on the Baltic Coast are presented. Some Norwegian populations are also described. Spontaneous introgression is found to be frequent. In environments with few ecological niches the process has gone very far, reaching replacement or complete fusion of populations. There is a general pattern of distribution in the Swedish rivers. *Pidschian, oxyrhynchus* and *peled* were the first invaders, already living in the Baltic Ice Lake, as did the ciscoes *albula* and *baunti* as well. Later on, probably first during the Litorina period, *lavaretus* and *nasus* entered the Baltic area and started a replacement process of the earlier arrivals. These, therefore, have mostly survived in the uppermost and most isolated lakes. All stages of the replacement can still be found in various lakes.

5. The European whitefish populations outside Scandinavia are reviewed and presented in Tables. The general pattern of the species and their mutual ousting and fusion in some localities is found to be similar to that of Scandinavia.

8. References

BEAN, T. H. 1889. Description of *Coregonus pusillus,* a new species of white fish from Alaska. *Proc. U.S. Nat. Mus. 11: 526.*

BERG, L. S. 1948—1949. Ryby presnykh vod SSSR i sopredelnykh stran. Ed. 4. I—III: 1—1382.

BLOCH, M. E. 1779. Naturgeschichte der Maräne. *Beschäftig. Berliner Ges. naturf. Freunde 4: 60—94.*

— 1783. Ökonomische Naturgeschichte der Fische Deutschlands. I. Berlin.

BROOKS, J. L. 1950. Speciation in ancient lakes. *Quart. Rev. Biology 25:30—60. 131—176.*

DYMOND, J. R. 1943. The Coregonine fishes of northwestern Canada. *Trans. Royal Canadian Institute XXIV (II): 171—231.*

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

ESCHMAYER, P. H. and R. M. BAILEY. 1955. The pygmy whitefish, *Coregonus coulteri,* in Lake Superior. *Trans. Amer. Fish. Soc. 84: 161—199.*

FABRICIUS, E. 1950. Heterogenous stimulus summation in the release of spawning activities in fish. *Report Inst. Freshwater Research, Drottningholm, 31: 57—99.*

FREIDENFELT, TH. 1933. Untersuchungen über die Coregonen des Wenersees. *Int. Rev. Hydrobiol. 30: 49—163.*

GMELIN, J. F. 1788. Linné: Systema naturae ed. XIII.

GRANLUND, E. 1930. De geografiska betingelserna för Stockholms uppkomst. *Ymer 50: 278—301.*

GRANLUND, J. 1955. Inlands- och östersjöfiske. Nordisk kultur. Fångst, jakt och fiske. Stockholm.

GÜNTHER, A. 1866. Catalogue of the Fishes in the British Museum. Vol. VI, London.

HILE, R. 1938. Morphometry of the cisco, *Leucichthys artedi* (LE SUEUR), in the lakes of the Northeastern Highlands, Wisconsin. *Intern. Rev. 36: 57—130.*

HUITFELDT-KAAS, H. 1924. Einwanderung und Verbreitung der Süsswasserfische in Norwegen, mit einem Anhang über den Krebs. *Arch. Hydrobiol. 14: 223—314.*

JÄRVI, T. H. 1928. Über die Arten und Formen der Coregonen s. str. in Finnland. *Acta Zool. Fennica 5: 1—259.*

— 1942. Die Bestände der kleinen Maränen (*Coregonus albula* L.) und ihre Schwankungen. I. Pyhäjärvi. *Acta Zool. Fennica 32: 1—89.*

— 1943. Zur Kenntnis der Coregonen-formen Nord-Finnlands, insbesondere des Kuusamo-Gebietes. *Acta Zool. Fennica 40: 1—91.*

— 1953. Über die Coregonen s. str. im Päijänne und in einigen anderen Gewässern Mittelfinnlands. *Acta Zool. Fennica 75: 1—33.*

— 1955. Über eingeführte Maränenbestände in einigen Kleingewässern der Gegend von Rovaniemi in Nordfinnland. *Acta Zool. Fennica 89: 1—74.*

JURINE, L. 1825. Histoire abregée des poissons du lac Léman. *Mem. Soc. Phys. Hist. nat. Genève 3: 133—235.*

KENNEDY, A. 1943. The whitefish, *Coregonus clupeaformis* (MITCHILL), of Lake Opeongo, Algonquin Park, Ontario. *Univ. Toronto Studies. Biol. Series LXII: 23—66.*

KOELZ, W. 1929. Coregonid fishes of the Great Lakes. *Bull. U.S. Bur. Fish. 43(2): 297—643.*

KULMATYCKI, W. J. 1926—1927. Studien an Coregonen Polens. *Arch. Hydrobiol. Ichthyol. Suwalki 1926—27: 275—375.*

— 1928. Beitrag zur Kenntnis der Coregonen Polens. *Arch. Hydrobiol. 19: 37—49.*

LINDROTH, A. 1957. A study of the whitefish (*Coregonus*) of the Sundsvall Bay district. *Report Inst. Freshwater Research, Drottningholm 38: 70—108.*

LINNAEUS, C. 1758. Systema Naturae. I. ed. X.

MANNSFELD, W. 1930. Studien an Coregonen des Ostbaltikums. *Arch. Hydrobiol. 21: 65—94.*

MARTIN, W. R. 1949. The mechanics of environmental control of body form in fishes. *Univ. Toronto Studies. Biol. Ser. 58: 1—91.*

MAYR, E. 1942. Systematics and the origin of species. New York.

MELLEN, I. M. 1923. The whitefishes (*Coregonus clupeaformis*) reared in the New York Aquarium. *Zoologica 2(17): 375—379.*

NÜSSLIN, O. 1882. Beiträge zur Kenntnis der *Coregonus*-Arten des Bodensees und einiger anderer nahegelegenen nordalpiner Seen. *Zool. Anz. 5: 86—306.*

NYSTRÖM, C. L. 1863. Iakttagelser rörande faunan i Jemtlands Vattendrag. Akad. avhandl. Stockholm.

OLOFSSON, O. 1934. Några inplanteringar av Lomsjö-sik. *Sv. Fiskeritidskr. 43: 4—8, 16—18, 43—47, 74—79.*

OTTERSTRÖM, C. V. 1922. Heltling (*Coregonus albula* L.) og Helt (*Coregonus lavaretus* L.) i Danmark. *Undersøgelser ferske vandes fiskeriforhold II, Kolding.*

Pallas, P. S. 1776. Reise durch verschiedene Provinzen des Russischen Reichs. III. St. Petersburg.

PETERS, W. 1874. Ene neue Art von Maränen, *Coregonus generosus,* aus dem Mark Brandenburg. *Monatsberichte der Königl. Preuss. Akad. Wiss. Zu Berlin 39: 790—795.*

PRAVDIN, I. F. 1931. Whitefishes (*Coregonus*) of the Lake District of the USSR. *Bull. Inst. of Ichthyology XII (fasc. 1) Leningrad: 166—235* (Russian, English Summary).

— 1954. Sigi Vodojemov Karelo-Finskoi SSR. Moskva-Leningrad.

REDEKE, H. C. 1934. Über den Rheinschnäpel, *Coregonus oxyrhynchus* L. *Verhandl. intern. Ver. theoret. u. angewandte Limnologie VI(2): 352—357.*

REGAN, C. T. 1908. A revision of the British and Irish fishes of the Genus Coregonus. *Ann. Mag. Nat. Hist. Lond. Ser. 8, Vol. 2: 482—490.*

RUNNSTRÖM, S. 1941. Vårlekande siklöja. *Sv. Fiskeritidskr. 50: 25—29.*

— 1944. Om smärlingen från några Jämtlandssjöar. *Sv. Fiskeritidskr. 53: 25—29.*

SMITT, F. A. 1886. Kritisk förteckning öfver de i Riksmuseum befintliga Salmonider. *Kongl. Svenska Vet. Akad. Handl. Bd 21 (8): 1—290.*

STEINMANN, P. 1950—1951. Monographie der schweizerischen Koregonen. *(Schweiz. Zeitschr. Hydrologie Vol. XII, fasc. 1, 2. Vol. XIII fasc. 1).* Verlag Birkhäuser, Basel.

SVÄRDSON, G. 1945. Chromosome studies on Salmonidae. *Report Inst. Freshwater Research, Drottningholm 23: 1—151.*

— 1949. The Coregonid Problem. I. Some general aspects of the problem. *Report Inst. Freshwater Research, Drottningholm 29: 89—101.*

— 1950. The Coregonid Problem. II. Morphology of two Coregonid Species in different environments. *Report Inst. Freshwater Research, Drottningholm 31: 151—162.*

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

— 1952. The Coregonid Problem. IV. The significance of scales and gillrakers. *Report Inst. Freshwater Research, Drottningholm 33: 204—232.*

— 1953. The Coregonid Problem. V. Sympatric whitefish species of the lakes Idsjön, Storsjön and Hornavan. *Report Inst. Freshwater Research, Drottningholm 34: 141—166.*

— 1954. Stora fiskbestånd eller bestånd av stora fiskar. *Sv. Fiskeritidskr. 63: 54—57.*

— 1956. Lambarfjärdens siklöja. *Sv. Fiskeritidskrift 65: 73—80.*

THIENEMANN, A. 1915. Untersuchungen an Coregonen. *Zeitschr. Fischeri. N. F. Bd. 1: 168—196.*

— 1922. Weitere Untersuchungen an Coregonen. *Arch. Hydrobiol. 13: 415—471.*

— 1926. Coregonen aus dem Ladogasee. *Vanamon Julkaisuja 6(7): 1—8.*

— 1928. Über die Edelmaräne (*Coregonus lavaretus* forma *generosus* PETERS) und die von ihr bewohnten Seen. *Arch. Hydrobiol. 19: 1—36.*

— 1935. Der Schnäpel (*Coregonus lavaretus balticus*) in Vorpommern. *Dohrniana Bd 14: 85—91.*

— 1953. Verbreitungsgeschichte der Süsswassertierwelt Europas. Die Binnengewässer Bd 18.

THOMPSON, W. 1835. Lough Neagh Coregonus. *Proc. Zool. Soc. London III: 77—78.*

VALENCIENNES, A. 1848. Histoire naturelle des poissons. Tom 21: 497.

WAGLER, E. 1937. Die Coregonen in den Seen des Voralpengebietes. IX. Die Systematik der Voralpencoregonen. *Int. Rev. Hydrobiol. 35: 345—446.*

— 1941. Die Coregonen. Handbuch der Binnenfischerei Mitteleuropas 3: 371—501.

WALTERS, V. 1955. Fishes of western Arctic America and Eastern Arctic Siberia. *Bull. Amer. Mus. Nat. Hist. 106(5): 261—368.*

WIDEGREN, HJ. 1863. Bidrag till kännedom om Sveriges Salmonider. *Öfversigt af Vetenskaps-Akad. Förhandlingar (1863): 1—78.*

WIESE, A. 1938. Die Grossmaränen Ostpreussens. *Zeitschrift Fischerei 35: 475—539.*

TABLES

Table 1. Gillrakers of transplanted whitefish populations

Population or pair	Date	16	17	18	19	20	21	22	23	24	25	26	27
Lake Dellen	Nov. 49—55	—	—	1	2	1	5	4	12	12	7	6	3
Lake Öjungen	Nov. 49	—	—	—	2	1	6	8	8	7	5	2	—
Indalsälven River[1]	Sep. 50—Nov. 53	—	—	—	—	—	—	—	—	—	2	8	14
Pond, Kälarne	1947	—	—	—	—	—	—	—	—	—	—	—	1
Lake Kölsjön	Oct. 55—56	—	—	—	—	—	—	—	—	1	—	3	11
Lake Idsjön	Oct. 47—Nov. 57	—	—	—	—	—	—	—	—	—	—	—	—
Pond, Kälarne	1945	—	—	—	—	—	—	—	—	—	—	—	—
»	1948	—	—	—	—	—	—	—	—	—	—	—	—
Lake Hållstasjön	Dec. 51—Feb. 52	—	—	—	—	—	—	—	—	—	—	—	—
Lake Öjingen	Oct. 55	—	—	—	—	—	—	—	—	—	—	—	—
Lake Målingen	Sep. 55	—	—	—	—	—	—	—	—	—	—	—	—
Pair: 32×32	1951—1956	—	—	—	—	—	—	—	—	—	—	—	1
Pair: 39×39	1951—1954	—	—	—	—	—	—	—	—	—	—	—	—
Pair: 41×41	1951—1955	—	—	—	—	—	—	—	—	—	—	—	—
Lake Åsnen, whitefish	Nov. 51	—	—	—	—	—	—	—	—	—	—	—	—
» , cisco	Nov. 51	—	—	—	—	—	—	—	—	—	—	—	—
F_1-hybrids, one summer old	1953	—	—	—	—	—	—	—	—	—	—	—	—
» , two summers old	1954	—	—	—	—	—	—	—	—	—	—	—	—
» , three summers old	1955	—	—	—	—	—	—	—	—	—	—	—	—
Lake Dikasjön, large whitefish	Oct. 48—Dec. 51	—	—	—	—	—	1	5	4	11	8	6	5
» , small »	Oct. 48—Dec. 51	—	—	—	—	—	—	—	—	—	—	—	—
F_1-hybrids, one summer old	1951	—	—	—	—	—	—	—	—	—	—	—	—
» , two summers old	1952	—	—	—	—	—	—	—	—	1	—	1	1
» , three summers old	1953	—	—	—	—	—	—	—	—	—	—	—	—
» , four summers old	1954	—	—	—	—	—	—	—	—	—	—	—	—
Lake Siljan, large whitefish	Aug. 48—Dec. 54	—	1	—	2	1	5	1	2	1	7	7	10
» , small »	Aug. 48—Dec. 54	—	—	—	—	—	—	—	—	—	—	1	5
F_1hybrids, one summer old	1953	—	—	—	—	—	—	—	—	—	—	—	1
» , two summers old	1954	—	—	—	—	—	—	—	—	—	—	—	—
Lake Uddjaur, shore-spawning	Dec. 53	1	2	4	5	3	2	—	—	—	—	—	—
» , stream-spawning	Dec. 53	—	—	—	—	—	—	—	—	—	—	—	—
F_1-hybrids, one summer old	1954	—	—	—	—	—	—	1	1	—	1	3	9
» , two summers old	1955	—	—	—	—	—	—	—	—	—	—	—	2
» , three summers old	1956	—	—	—	—	—	1	—	—	—	—	5	17
Lake Brunträsket, large	Oct. 48—Jan. 52	1	—	—	2	5	7	16	19	10	16	12	9
Lake Stora Skeppträsket, small	Dec. 46—54	—	—	—	—	—	—	—	—	—	—	—	—
F_1-hybrids, one summer old	1952	—	—	—	—	—	—	—	—	—	—	—	—
» , two summers old	1953	—	—	—	—	—	—	—	—	—	—	—	1
» , three summers old	1954	—	—	—	—	—	—	—	—	—	—	—	—
» , five summers old	1956	—	—	—	—	—	—	—	—	—	—	—	—
F_2-hybrids, one summer old	1955	—	—	—	—	—	—	—	—	—	—	1	2
» , two summers old	1956	—	—	—	—	—	—	—	—	—	—	1	3

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[1] Includes material from LINDROTH (1957).

and of the progeny from selected pairs or crossed species.

28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	Sample	Mean
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	53	23.5
—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	40	23.0
35	60	78	79	60	54	36	15	10	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	455	31.0
3	5	6	10	8	3	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	38	30.8
18	17	35	34	37	28	14	7	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	206	30.9
—	3	3	12	35	61	95	110	137	134	91	66	28	18	6	1	—	—	—	—	—	—	—	—	800	36.0
—	—	1	1	5	4	9	19	21	21	14	3	2	—	—	—	—	—	—	—	—	—	—	—	100	35.9
—	—	—	—	—	2	4	4	8	9	8	8	1	1	—	—	—	—	—	—	—	—	—	—	45	36.9
—	—	—	—	—	1	2	2	4	2	3	1	2	—	—	—	—	—	—	—	—	—	—	—	17	36.6
—	—	—	—	4	6	1	1	1	2	1	2	1	4	2	—	—	—	—	—	—	—	—	—	25	36.4
—	—	—	—	2	2	2	4	10	4	1	—	1	1	—	—	—	—	—	—	—	—	—	—	27	35.7
—	—	4	9	14	19	19	10	13	4	2	2	1	1	—	—	—	—	—	—	—	—	—	—	99	33.8
—	—	—	—	—	—	—	1	—	—	1	2	1	2	—	—	—	—	—	—	—	—	—	—	7	39.0
—	—	—	—	—	—	—	3	5	5	9	6	8	3	1	—	—	—	—	—	—	—	—	—	40	38.3
—	—	—	—	1	4	5	9	20	10	6	2	1	—	—	—	—	—	—	—	—	—	—	—	58	35.9
—	—	—	—	—	—	—	—	—	—	2	1	1	5	8	10	12	6	3	2	1	—	—	—	51	43.2
—	—	—	—	—	1	5	11	13	33	35	20	16	11	7	3	—	2	—	—	—	—	—	—	157	38.2
—	—	—	—	—	—	—	3	—	10	4	7	2	8	9	3	2	—	2	—	—	—	—	—	50	39.9
—	—	—	—	1	—	—	2	7	10	11	16	5	3	1	2	2	2	—	—	—	—	—	—	62	38.6
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	41	24.5
—	—	—	1	3	—	2	8	17	19	27	21	25	19	13	7	2	1	1	—	—	—	—	—	166	38.8
—	—	3	5	5	4	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	32.0
2	5	6	10	27	35	31	20	8	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	150	33.0
3	1	9	19	51	33	47	17	12	3	3	—	—	—	—	—	—	—	—	—	—	—	—	—	198	33.0
2	4	10	26	27	41	34	17	10	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	172	32.8
16	16	13	5	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	91	27.3
3	—	6	5	7	8	16	25	12	12	5	1	—	—	—	—	—	—	—	—	—	—	—	—	107	33.8
2	1	6	3	6	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23	30.9
—	—	5	9	3	3	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23	31.6
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	17	18.8
—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	3	6	2	1	7	4	1	1	—	26	45.7
8	7	11	8	4	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	56	29.0
3	2	5	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	29.4
27	17	19	12	9	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	112	29.1
6	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	105	23.9
—	—	—	—	—	—	1	4	9	34	57	65	84	55	45	22	9	3	1	—	—	—	—	—	389	39.8
—	—	—	5	7	12	7	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	35	33.0
1	—	6	11	20	28	30	20	16	8	—	—	—	1	—	—	—	—	—	—	—	—	—	—	142	33.6
—	1	2	5	14	14	15	20	7	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	80	33.6
—	—	1	—	1	1	—	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	33.7
2	7	12	7	5	9	2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	50	30.9
1	6	17	17	13	7	7	3	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	77	31.3

Table 2 a. Gillrakers in whitefish samples from the Swedish coast of the Baltic Sea.

Locality	Date	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	Sample	Mean
Torne River	Sep. 56	—	—	—	—	—	—	—	—	—	—	4	2	5	1	—	—	—	—	—	—	—	—	12	30.3
Kalix River	Oct. 56	—	—	—	—	—	—	2	4	18	15	23	13	16	12	10	4	2	—	—	—	—	—	119	29.7
Storö-hamn	Oct. 52—56	—	—	2	2	4	6	11	8	7	4	4	5	—	—	—	—	—	—	—	—	—	—	53	25.9
Hastaskär	Oct. 52—54, Jun. 56	—	—	—	—	3	2	4	6	14	17	16	17	13	11	5	5	1	1	—	—	—	—	115	29.2
Råne River	Oct. 49—51	—	—	—	—	—	—	4	3	8	10	13	16	15	8	3	1	—	—	—	—	—	—	81	29.4
Lule River	Oct. 49	—	—	—	—	—	1	3	5	3	10	5	5	8	2	1	1	—	—	—	—	—	—	44	28.7
Sandö	Nov. 53	—	—	—	2	4	8	20	18	19	9	6	5	2	1	—	—	—	—	—	—	—	—	94	26.4
Germandö	Oct. 53	—	—	—	1	—	3	1	2	2	1	1	—	—	—	—	—	—	—	—	—	—	—	11	25.6
Junkö	Jun. 51	—	—	—	1	1	5	8	9	11	7	7	13	7	7	1	3	1	1	—	—	—	—	82	28.4
Rödkallen	Nov. 51	—	—	1	3	7	10	12	12	20	14	11	4	1	—	2	1	—	—	—	—	—	—	98	26.6
Pite River	Oct. 54	—	—	—	1	4	11	9	22	19	14	1	4	2	3	1	—	—	—	—	—	—	—	91	26.6
Skellefte River	Nov. 56	—	—	1	—	—	1	—	—	1	3	4	1	—	1	—	—	—	—	—	—	—	—	12	27.8
Bure River	Oct. 48	—	—	—	—	—	1	6	15	11	17	16	13	12	6	1	—	—	—	—	—	—	—	98	28.4
Björöklubb	Nov. 48	—	—	—	4	6	13	18	21	17	13	5	1	—	1	—	—	—	—	—	—	—	—	99	25.9
Gumboda	Nov. 51	—	—	—	—	1	1	2	10	15	12	5	2	1	—	—	—	1	—	—	—	—	—	50	27.4
Sikeå	Nov. 51	—	—	—	—	1	4	4	8	12	12	3	6	1	—	—	—	—	—	—	—	—	—	51	27.2
Holmön	Nov. 51	—	—	—	—	—	—	2	3	4	3	1	2	—	—	—	—	—	—	—	—	—	—	15	27.3
Ume River	Nov. 55	—	1	—	—	—	8	12	17	18	27	8	7	6	4	—	1	—	—	—	—	—	—	109	27.4
Sörmjöle	Nov. 51	—	—	—	—	1	—	—	2	5	2	3	1	—	1	—	—	—	—	—	—	—	—	15	27.7
Öre River	Nov. 55	—	—	—	—	—	—	—	—	4	6	11	15	9	5	1	1	—	—	—	—	—	—	52	29.8
Gide River	Oct. 54	—	—	—	—	1	4	2	16	7	10	5	5	4	—	1	—	—	—	—	—	—	—	55	27.4
Trysunda	Nov. 51	—	—	—	—	—	—	—	3	2	—	2	2	—	—	—	—	—	—	—	—	—	—	9	27.8
Ångermanälven River	Oct.—Dec. 55	—	—	—	1	—	1	3	4	10	20	22	28	26	33	19	12	6	—	3	1	—	—	189	30.6
Åvike [1]	Oct. 51	—	—	—	—	—	2	5	9	10	3	8	11	2	—	—	—	—	—	—	—	—	—	50	27.7
Alnö [1]	Nov. 51—53	—	—	—	—	—	2	5	19	13	8	6	1	2	3	1	—	—	—	—	—	—	—	60	27.3
Indalsälven River [1]	Sep. 51—Nov. 53	—	—	—	—	—	—	2	8	14	32	53	70	71	52	44	31	14	10	4	—	—	—	405	31.0
» »	Nov. 50	—	—	—	—	—	—	—	—	—	3	7	8	8	8	10	5	1	—	—	—	—	—	50	31.3
Bergafjärden [1]	Oct. 51—Nov. 53	—	—	—	—	—	3	10	16	21	23	17	5	3	2	—	—	—	—	—	—	—	—	100	27.5
Ljungan River [1]	Sep. 51—52	—	—	—	—	—	—	—	1	4	5	19	17	20	18	10	13	3	—	—	—	—	—	110	31.0
Långvindsbruk	Nov. 55	—	—	—	—	—	1	1	4	3	6	3	—	1	—	1	—	—	—	—	—	—	—	20	27.7
Ljusnan River [1]	Oct. 52	—	—	—	—	—	1	—	1	2	1	5	7	12	7	3	6	2	2	1	—	—	—	50	31.3
Granö	Nov. 51	—	—	—	1	—	—	1	1	7	4	7	2	5	2	—	—	—	—	—	—	—	—	30	28.5
Dalälven River	Nov. 56	—	—	—	—	—	—	—	6	5	1	8	11	10	4	3	6	4	3	—	1	—	—	62	30.8
Spillersboda	Nov. 50	—	—	—	—	—	—	2	3	3	9	8	7	6	1	—	1	—	—	—	—	—	—	40	28.9
Edö	Nov. 51	—	—	—	—	—	—	—	2	2	5	7	4	2	5	1	1	—	1	—	—	—	—	30	29.8
Lake Mälaren [2]	Nov. 50—55	—	—	—	—	—	—	—	—	—	4	7	15	9	9	10	6	—	—	—	—	—	—	60	31.1
Oxelösund	Nov. 51	—	—	—	—	—	—	1	1	6	5	4	4	4	—	—	—	—	—	—	—	—	—	25	28.5
Västervik	Nov. 49—50	—	—	—	—	—	—	6	7	12	24	25	20	10	6	3	1	—	—	—	—	—	—	114	28.8
Pataholm	Nov. 51	—	—	—	—	—	1	—	1	5	3	2	1	—	—	—	—	—	—	—	—	—	—	13	27.5
Gualöv	Nov. 51	—	—	—	—	—	2	2	1	6	7	4	—	—	—	—	—	—	—	—	—	—	—	22	27.2
Gotland	Nov. 50—Feb. 56	1	3	6	16	17	20	15	10	2	1	—	—	—	—	—	—	—	—	—	—	—	—	91	23.6

Total: 2.886 specimens

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[1] Data from LINDROTH (1957).

[2] Lake Mälaren was part of the Baltic up to 1100 A.D. and though the land has been raised 3—4 metres since this time, the height of Lake Mälaren has, through erosion, remained only 35—40 cm above average sea level (GRANLUND 1930).

Table 2 continues on next page.

Table 2 b. Whitefish samples from the eastern

Locality	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Kemi River[1]	—	—	—	—	—	—	—	—	—	—	—	3	3	3
Pyhäjoki River[2]	—	—	—	—	—	—	—	—	1	2	—	—	2	3
Kalajoki River[1][2]	—	—	—	—	—	1	—	1	6	5	4	8	8	3
Kokkola[1]	—	—	—	—	—	—	—	—	2	1	5	3	1	3
Kokemäki River[2]	—	—	—	—	—	—	—	—	—	1	—	4	3	7
Luvia[2]	—	—	—	—	—	—	—	—	—	—	1	1	3	—
Pyhämaa[2]	—	—	—	—	—	—	—	—	—	—	4	7	11	18
Kymi River[2]	—	—	—	—	—	—	—	—	—	—	—	4	5	6
Finnish Bay, off Neva[3]	—	—	—	—	—	—	—	2	2	3	1	1	3	1
Neva River[3]	—	—	—	—	—	—	1	5	13	8	13	—	3	2
Lake Ladoga[3]	—	—	—	—	5	9	21	35	43	46	21	7	3	2
» »[4]	—	—	—	—	—	—	—	—	—	—	—	[———		
Finnish Bay, Luga[5]	—	—	—	—	—	—	[———							
Riga Bay[6]	—	—	1	—	1	2	4	9	6	3	1	—	—	—
» »[6]	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Off Salis River[6]	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Kurisches Haff[7]	—	—	—	—	—	—	—	—	—	—	—	[———		
Hela[8]	1	1	3	8	9	4	—	4	4	—	—	—	—	—
Pomeranian coast[9]	—	—	—	—	—	—	—	—	—	—	—	[———		
Schlei River[10]	—	—	—	—	—	—	—	—	—	1	1	1	2	1

[1] JÄRYI (in litt.). [2] JÄRVI (1928). [3] PRAVDIN (1931). [4] Combined from PRAVDIN (1954) and THIENEMANN (1926), Lake Ladoga was included in the Baltic Sea up to 2.000 years ago (PRAVDIN 1954). [5] BERG (1948). [6] MANNSFELD (1930) [7] WIESE (1938). [8] KULMATYCKI (1927), the figures probably too low, due to another counting practice. [9] THIENEMANN (1935). [10] THIENEMANN (1922)

and southern coast of the Baltic Sea.

30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	Sample	Mean
9	7	8	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	38*	30.6
1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	27.9
7	3	5	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	54*	27.9
4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20*	27.5
8	4	4	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	35	29.8
3	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	29.0
13	3	6	2	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	68	29.4
9	6	8	4	4	3	—	1	—	—	—	—	—	—	—	—	—	—	—	50	30.9
—	1	—	—	—	—	—	—	—	13	1	3	2	6	—	—	2	1	—	42	(26.1) (41.1)
—	—	—	—	1	—	—	1	—	2	2	8	13	4	3	6	2	3	4	95	(25.1) (42.9)
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	193	24.1
—	—	—	—	—	—	—	—	—	—]	—	—	—	—	—	—	—	—	—	c:a 40	33
—	—	—	—]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	112	27.6
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	27*	23.0
—	2	4	1	4	3	1	—	2	—	—	—	—	—	—	—	—	—	—	17*	33.9
—	—	—	—	—	—	—	—	—	—	8	3	1	—	—	—	—	—	—	12*	40.4
—	—	—	—	—	—	—	—	—	—]	—	—	—	—	—	—	—	—	—	65	33.4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	34*	20.3
—	—]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	28.5
1	2	7	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	21*	30.7

* Means that the gillrakers were counted on the first arch on both sides; the sample is thus twice the number of fish.

Table 3. Whitefish samples from

Lake, locality	Date	Size	17	18	19	20	21	22	23	24	25	26	27
Torne River system													
Nakerijärvi	Oct. 56	—	—	—	—	1	—	1	5	1	7	6	10
Torneträsk	Oct. 51—Nov. 54	—	—	—	—	—	—	1	8	16	30	62	64
Jukkasjärvi	Sep. 56	< 150	—	—	—	—	—	—	—	—	—	—	—
»	Sep. 56	> 150	—	—	—	—	—	1	1	4	11	10	14
Sautusjärvi	Sep. 56	—	2	3	1	1	1	—	—	2	3	6	2
Lainio River													
Kuormakkajärvi	Sep. 56	—	—	—	—	—	—	—	3	12	13	3	7
Muonio River													
Stuorrajavre[1]	Oct. 53—54	—	—	—	—	2	8	10	14	36	32	19	19
Gåskinjavre[1]	Oct. 53	—	—	—	—	—	2	3	5	8	12	8	7
Idijärvi	Dec. 56	—	—	—	—	—	—	—	—	—	—	—	—
Märtäjärvi	Oct. 56	—	—	—	—	—	—	—	—	—	1	—	4
Särkijärvi[2]	1931	—	—	—	—	—	—	—	—	—	—	—	—
Kukkola, at the mouth	Sep. 56	—	—	—	—	—	—	—	—	—	—	—	—
Kalix River system													
Paittasjärvi	Oct. 56	—	—	1	1	2	17	9	19	12	9	5	1
Kaalasjärvi	Sep. 56	—	—	—	—	2	9	10	32	40	43	38	22
Kaitum River													
Pauki	Dec. 51	< 180	—	—	—	—	—	—	—	—	—	—	—
»	Oct.—Nov. 56	—	—	—	—	—	1	2	6	11	9	14	4
Tjautjasjärvi	Sep. 56	—	—	—	1	6	6	13	8	6	5	3	3
Akkajärvi	Oct. 56	—	—	1	3	6	9	14	17	5	5	—	—
Ängesån River													
Vettasjärvi	Jan. 42—Feb. 57	—	—	—	—	—	—	—	—	—	—	—	1
Lina River													
Saivo	Nov. 51	—	—	—	—	—	—	—	2	4	13	15	13
»	Mar. 51—56	—	—	—	—	—	—	—	1	3	5	9	19
Kamlunge, at the mouth	Oct. 56	—	—	—	—	—	—	—	—	—	2	4	18

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[1] These Norwegian lakes nowadays flow, through the Alter River, to the Atlantic Ocean. Their whitefish populations, however, are regarded as postglacial invaders from the Baltic.

[2] From JARVI (1943, p. 69); the lake is situated in Finland.

the Torne and Kalix River systems.

28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	Sample	Mean
10	12	10	10	7	9	4	5	4	—	2	2	—	—	—	—	—	—	106	29.7
47	40	31	11	6	1	—	—	—	—	—	—	—	—	—	—	—	—	317	27.3
—	—	—	—	—	—	—	—	1	4	4	3	—	—	—	—	—	—	12	37.8
12	14	5	5	3	2	1	—	—	—	—	—	—	—	—	—	—	—	88	27.9
15	18	9	2	1	—	2	—	—	—	—	—	—	—	—	—	—	—	68	(18.5) (28.5)
2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	40	25.1
4	6	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	152	24.8
1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	47	24.9
—	—	2	6	19	11	13	11	4	1	1	2	—	—	—	—	—	—	70	33.4
13	6	8	10	9	6	2	2	—	—	—	—	—	—	—	—	—	—	61	30.2
—	1	—	—	2	2	—	—	—	—	—	—	—	—	—	—	—	—	5	31.8
—	4	2	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	12	30.3
4	—	—	—	—	—	—	1	2	2	3	3	5	2	—	—	—	—	98	(23.1) (38.6)
13	3	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	216	24.9
—	1	1	2	2	1	1	—	—	—	—	—	—	—	—	—	—	—	8	31.5
5	5	1	—	1	—	—	1	—	—	1	—	1	—	—	—	—	—	62	26.2
2	2	5	4	2	2	—	2	—	4	4	10	10	10	7	5	1	1	122	(—) (40.1)
—	1	3	4	5	5	1	1	3	—	1	6	7	3	3	4	1	2	110	(22.1) (—)
2	4	12	15	10	6	3	2	—	—	—	—	—	—	—	—	—	—	55	31.2
11	5	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	66	26.6
9	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	51	26.7
15	23	13	16	12	10	4	2	—	—	—	—	—	—	—	—	—	—	119	29.7

Total: 1.885 specimens

Table 4. Whitefish samples from the Råne,

Lake, locality	Date	Size	16	17	18	19	20	21	22	23	24
									Gill-		
Råne River											
Degervattnet	Oct. 49—Nov. 53	—	4	4	11	20	16	18	10	3	2
Råneå, at the mouth	Oct. 49—51	—	—	—	—	—	—	—	—	—	—
Pite River											
Tjeggelvas	Jan. 55	—	—	—	—	—	—	—	—	—	—
Skärfajaure	Jan. 52	—	—	—	—	—	—	—	1	2	3
»	Dec. 54	—	—	—	—	—	—	—	—	—	—
Måskejaure	Jan. 52	—	—	—	—	—	—	—	—	—	—
Suddesjaure	Dec. 56	—	—	2	—	2	1	—	1	—	—
Malmesjaure	Nov. 49—Oct. 52	—	—	1	—	—	—	—	—	—	1
Sleng	Oct. 56	—	—	1	—	—	—	3	—	—	—
Piteå, at the mouth	Oct. 54	—	—	—	—	—	—	—	1	4	11
Åby River											
Lauker	Oct. 56	—	—	—	—	2	4	4	8	4	2
Byske River											
Långträsket	Aug. 51	< 280	—	—	—	—	—	—	—	—	—
»	Aug. 51	> 280	—	—	2	1	—	—	1	—	—
Gråträsket	Jan. 55	< 250	—	—	—	—	—	—	—	—	—
»	Jan. 55	> 250	1	5	10	20	18	21	9	4	—
»	Jan. 56	—	1	4	9	10	12	7	2	1	—

Pite, Åby and Byske River systems.

rakers																	
25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	Sample	Mean
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	88	19.8
4	3	8	10	13	16	15	8	3	1	—	—	—	—	—	—	81	29.4
—	—	1	2	2	4	9	13	19	10	6	5	4	2	—	—	77	32.9
4	—	—	—	—	—	—	2	2	1	1	3	1	—	—	—	20	(24.0) (34.4)
—	—	—	—	—	7	10	18	19	21	16	7	6	3	1	—	108	33.6
—	—	—	1	—	1	—	1	1	—	—	1	—	—	—	—	5	31.8
—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	8	(19.0) (—)
3	—	—	—	4	1	1	2	6	4	2	2	1	1	—	—	29	(—) (33.0)
—	—	1	—	—	4	3	4	13	10	15	4	6	2	1	—	67	(20.0) (34.0)
9	22	19	14	1	4	2	3	1	—	—	—	—	—	—	—	91	26.6
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	30	22.1
—	—	—	—	—	—	—	3	1	4	4	1	1	1	1	1	17	35.0
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	19.3
—	—	1	1	1	—	2	1	1	—	—	—	—	—	—	—	7	30.1
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	88	19.9
—	—	2	1	3	2	3	—	2	—	—	—	—	—	—	—	59	(19.3) (29.8)

Total: 779 specimens

Table 5. Whitefish samples

Lake, locality	Date	Size	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Råtjajaure	Sep. 56	—	—	—	—	—	—	—	—	—	—	2	4	6	13	12	8
Luoktanjarkajaure[1] .	Aug. 28	—	—	—	—	—	—	—	—	—	—	—	1	1	7	8	7
»	Jul. 53	—	—	—	—	—	—	—	—	—	—	1	3	4	10	13	10
Alemusjaure[1]	Aug. 28	—	—	—	—	—	—	—	—	—	—	1	—	—	5	6	12
»	Jul. 56	—	—	—	—	—	—	—	—	—	—	2	3	5	5	9	3
Kårtjejaure[1]	Aug. 28	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
Langas	Jul. 53—Sep. 54	—	—	—	—	—	—	—	—	1	3	6	2	1	1	2	3
St. Lulejaure	Jul. 53—Aug. 55	< 400	—	—	—	1	—	4	7	17	25	28	46	30	34	15	12
»	Oct. 51	> 400	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
Lilla Lule River																	
Peuraure	Nov. 56	—	—	—	3	3	5	9	11	6	8	5	1	2	—	—	—
Karats	Nov. 56—Mar. 57	—	2	2	13	13	19	26	22	20	14	6	—	1	1	—	1
Saggat	Dec. 56	< 200	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
»	Dec. 56	> 200	—	1	1	3	3	4	2	4	4	1	1	1	—	—	—
Skalka	Nov. 56	< 400	—	—	1	2	3	2	1	—	—	—	—	1	—	—	—
»	Nov. 56	> 400	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Parkijaure	Jan. 57	—	—	2	—	1	1	2	3	—	—	1	2	1	2	1	—
Randijaure	Nov. 51—Dec. 56	—	—	—	3	8	5	5	1	2	3	3	—	—	—	—	—
Vaikijaure	Nov. 56	< 200	—	—	—	—	—	—	—	—	2	1	2	4	5	5	7
»	Nov. 56	> 200	—	—	1	1	4	2	4	5	7	1	1	1	—	—	—
Lule river, mouth ..	Oct. 49	—	—	—	—	—	—	—	1	3	5	3	10	5	5	8	2

[1] Unpublished data through the courtesy of Dr. STEN VALLIN.

from the Lule River system.

33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	Sample	Mean
3	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	50	30.5
5	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	31	31.4
6	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	50	31.0
2	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	29	31.6
1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	29	30.2
5	3	3	1	3	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	18	34.8
2	5	4	4	6	1	1	2	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	47	33.2
5	8	3	2	4	—	2	3	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	279	29.6
—	—	—	1	3	6	1	5	2	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	22	(39.2)
—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	54	(24.2)
1	1	1	—	—	—	—	1	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	146	(23.3)
1	—	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	35.0
—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	2	2	2	1	2	1	2	—	—	1	41	(23.8) (50.4)
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	22.7
—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	1	—	1	—	—	—	1	—	—	—	6	48.5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	25.1
1	3	3	3	2	—	1	1	2	1	1	—	2	2	1	2	4	1	—	—	1	—	—	—	—	61	(22.9)
6	5	3	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	43	31.7
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	27	24.5
1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	44	28.7

Total: 1.007 specimens

Table 6. Whitefish samples from

Lake, locality	Date	Size	16	17	18	19	20	21	22	23	24	25	26	27	28
Sakkaträsk	Jan. 52—54	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Jutis	Dec. 49—Oct. 54	—	3	8	19	33	32	26	20	8	1	1	—	—	—
Akkelisjaur	Jan. 50	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hornavan	1944—1954	< 170	—	—	—	—	—	1	—	—	1	—	—	1	—
»	1944—1954	170—200	—	—	—	—	—	—	—	—	—	—	1	—	—
»	1944—1954	201—250	—	—	1	2	—	1	1	—	1	2	2	3	3
»	1944—1954	251—350	2	1	6	12	11	13	11	6	4	4	3	6	6
»	1944—1954	> 350	—	—	6	7	4	6	5	4	3	—	—	1	2
Uddjaur	1944—1954	< 170	—	—	3	2	2	—	—	—	—	—	—	—	—
»	1944—1954	170—200	—	—	1	—	—	—	—	—	—	—	—	—	—
»	1944—1954	201—250	—	—	—	1	—	—	—	—	—	—	—	—	—
»	1944—1954	251—350	2	5	11	17	14	9	1	—	1	—	—	—	—
»	1944—1954	> 350	3	1	13	13	15	3	1	1	—	1	—	—	—
Storavan	1950—1954	< 170	—	—	—	—	—	—	—	—	—	—	—	1	1
»	1950—1954	170—200	—	—	—	—	—	—	1	—	—	—	—	—	—
»	1950—1954	201—250	—	—	3	5	—	3	—	—	—	—	—	—	—
»	1950—1954	> 251	4	8	12	18	7	7	—	2	—	1	—	—	—
Kokträsk	Dec. 50—Jan. 53	—	—	—	—	—	—	—	—	—	—	—	—	—	—
»	Jan. 53	—	—	—	—	—	—	—	—	—	—	1	—	—	1
Stenträsk	Nov. 56	—	—	—	—	—	—	—	2	—	—	1	2	—	—
Vågträsk	Jan. 52	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bockträsk	Jan. 53	—	—	—	—	—	—	—	—	—	—	1	—	—	1
Ö. Verbosjön	Jan. 53	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Brunträsket	Oct. 48—Jan. 52	—	1	—	—	2	5	7	16	19	10	16	12	9	6
»	Oct. 48—53	—	—	—	—	2	5	6	1	6	13	25	57	52	74
Lajnijaur	Oct. 48—53	—	—	—	—	—	—	1	—	1	—	5	8	14	15
»	Jan.—Dec. 53	—	—	2	6	6	2	2	—	—	—	—	—	—	—
St. Skeppträsket[1] ...	Aug. 13	> 220	—	—	—	—	—	—	—	—	—	—	—	—	—
»[2] ...	Aug. 13	< 220	—	—	—	—	—	—	—	—	—	—	—	—	—
» ...	Dec. 46—54	< 220	—	—	—	—	—	—	—	—	—	—	—	—	—
» ...	Oct. 55	> 220	—	—	—	—	—	—	—	—	—	—	—	1	8
L. Skeppträsket	Dec. 55	< 250	—	1	1	—	4	4	2	2	4	1	—	—	—
»	Dec. 55	251—300	—	2	4	5	12	15	11	9	5	—	3	—	—
»	Dec. 55	> 300	—	1	—	1	1	2	1	—	1	—	—	—	—
Malåträsk[1]	Aug. 13	—	—	—	—	—	—	—	—	—	—	—	1	—	—
River Malå	Dec. 53	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Kvammarn	Nov. 51	—	—	—	—	—	—	—	—	—	—	—	—	—	—
At the mouth	Nov. 56	—	—	—	—	—	—	1	—	—	1	—	—	1	3
Bure river mouth[3] ..	Oct. 48	—	—	—	—	—	—	—	—	—	1	6	15	11	17

[1] From unpublished notes by Dr. NILS ROSÉN.

[2] Material preserved in the Museum of Gothenburg.

[3] Fry from this population has been introduced in the 1940's into the Lakes Brunträsket, Lajnijaur, St. Skeppträsket and other lakes within the Skellefte River system.

the Skellefte River system.

29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	Sample	Mean
—	—	1	—	—	1	3	4	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	12	35.7
—	—	—	—	—	—	—	2	2	—	1	1	—	—	—	—	—	—	—	—	—	—	—	157	(19.9) (37.5)
1	3	9	5	11	14	12	6	3	7	2	—	—	—	—	—	—	—	—	—	—	—	—	73	34.1
2	12	20	32	51	53	55	41	29	19	9	1	2	—	—	—	—	—	—	—	—	—	—	329	34.3
—	—	3	4	6	11	11	21	21	29	28	25	9	6	—	—	—	—	—	—	—	—	—	175	37.4
4	3	1	2	4	8	9	13	13	15	11	8	4	1	—	—	—	—	—	—	—	—	—	112	—
2	2	1	1	4	3	3	1	—	1	—	1	—	1	—	—	—	—	—	—	—	—	1	106	—
2	—	—	—	—	1	—	—	1	1	—	—	—	1	—	—	—	—	—	1	—	1	—	46	—
—	1	2	5	6	4	11	10	9	7	2	—	—	1	2	3	2	—	1	—	—	—	—	75	(35.2)
—	—	2	4	6	9	3	5	4	4	1	—	—	—	—	—	—	—	—	—	—	—	—	39	(34.7)
—	—	—	1	1	3	—	2	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	9	—
—	—	—	—	—	—	—	—	—	—	—	2	3	3	2	3	5	3	2	5	1	—	2	91	(19.2) (45.0)
—	—	—	—	—	—	—	—	—	—	1	—	1	3	3	8	2	5	7	3	—	1	2	87	(19.2) (45.3)
—	3	14	18	22	44	23	18	7	5	1	2	—	—	—	—	—	—	—	—	—	—	—	159	33.9
2	1	1	2	—	3	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13	—
—	1	—	—	2	—	—	—	—	1	—	—	—	—	—	—	—	1	—	—	—	—	—	16	—
—	1	1	—	—	1	—	—	—	—	—	2	—	—	3	6	4	1	7	5	1	2	—	93	(18.9) (45.7)
—	—	1	8	12	13	13	12	5	2	—	—	—	—	—	—	—	—	—	—	—	—	—	66	34.4
3	6	5	3	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	30.4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	24.2
—	—	1	2	2	4	4	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	17	34.2
5	7	8	8	5	2	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	40	31.3
—	—	—	—	—	—	—	1	1	—	4	4	2	1	—	—	—	—	1	—	—	—	—	14	40.0
1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	105	23.9
62	30	27	10	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	381	27.7
15	13	11	8	3	4	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	99	29.0
—	—	1	1	3	1	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	29	(18.8) (33.8)
—	—	1	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	33.0
—	—	—	—	—	—	—	1	3	4	5	6	5	3	2	2	—	—	—	—	—	—	—	31	40.0
—	—	—	—	—	1	4	9	34	57	65	84	55	45	22	9	3	1	—	—	—	—	—	389	39.8
6	3	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	29.0
—	—	1	—	5	7	7	6	4	4	2	—	—	—	1	—	—	—	—	—	—	—	—	56	(21.6) (35.6)
—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	67	(21.3)
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	20.6
1	—	1	1	5	8	5	4	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	28	33.9
—	2	3	—	1	1	3	8	4	2	—	—	2	—	—	—	—	—	—	—	—	—	—	26	35.3
—	—	1	2	2	3	6	2	4	2	4	6	5	2	—	—	—	—	—	—	—	—	—	39	37.3
4	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12	27.8
16	13	12	6	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	98	28.4

Total: 3.046 specimens

Table 7. Whitefish samples

Lake, locality	Date	Size	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Laisälven River																	
Storlaisan	Sep. 56	—	2	9	20	23	45	39	31	12	9	4	1	1	—	—	—
»	Oct. 56	—	—	—	—	—	—	13	24	21	25	11	8	—	—	—	—
Vindelälven River																	
Övre Gautsträsk ..	Nov. 54	—	—	—	—	—	—	—	—	—	—	—	2	—	2	3	4
Gertsträsk	Dec. 55	—	—	—	—	—	—	—	—	—	—	—	3	2	6	14	14
Storvindeln	Feb. 52—Dec. 53	< 160	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
»	Dec. 51—Nov. 53	160—300	—	2	1	3	11	6	1	2	—	—	—	1	—	—	—
»	Nov. 53—Dec. 56	> 300	—	—	2	2	11	20	28	25	21	11	12	5	—	1	—
Svergoträsk	Oct. 49	—	—	—	—	—	1	1	4	3	—	1	—	—	1	—	—
Juktån River																	
Fjosokken	Nov. 53	—	—	—	—	—	—	—	1	4	4	6	4	5	1	—	—
Ume River																	
Nedre Björkvattnet	Sep. 54	—	—	—	—	—	1	—	2	2	3	9	8	8	6	4	1
Storuman	Nov. 53—54	< 200	—	—	—	—	—	2	2	2	1	—	—	—	1	—	—
» , north ..	Nov. 53—54	> 200	—	1	1	7	7	20	12	22	16	7	3	1	1	—	—
» , south ..	Nov. 53	> 200	—	—	—	1	3	5	4	8	8	9	8	1	3	—	—
Stensele	Nov. 53—Dec. 54	—	—	—	—	2	2	3	2	4	17	10	19	18	9	6	4
Umgransele	Sep. 54	—	—	—	—	—	—	—	—	—	1	3	2	2	7	3	2
Bålforsen	Sep. 54	—	—	—	—	—	—	—	—	—	—	1	2	2	2	1	—
Sikträsket	Nov. 55	—	—	—	—	—	—	—	—	1	11	12	8	15	5	—	1
Falträsket	Sep. 55	—	—	—	—	—	2	4	13	12	13	6	2	—	—	—	—
At the mouth	Nov. 55	—	—	—	—	—	1	—	—	—	8	12	17	18	27	8	7

from the Ume River system.

31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	Sample	Mean
—	—	1	—	—	—	—	—	—	3	6	6	7	7	8	7	9	3	11	11	3	6	3	2	2	291	(20.6) (46.9)
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	102	23.2
6	11	13	10	7	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	64	32.6
13	24	11	7	3	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	99	31.1
—	—	—	—	1	8	16	22	27	22	20	13	7	2	2	1	—	—	—	—	—	—	—	—	—	141	39.5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	27	20.4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	138	22.9
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	22.8
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	25	25.1
2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	46	26.2
—	—	—	—	—	—	—	1	3	7	21	36	39	39	44	20	22	4	2	2	—	—	—	—	—	248	(23.0) (43.9)
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	98	22.3
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	50	23.8
1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	99	25.8
1	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23	28.0
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	27.0
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	53	25.8
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	51	23.1
6	4	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	109	27.4

Total: 1.683 specimens

Table 8. Whitefish samples from

Lake, locality	Date	Size	16	17	18	19	20	21	22	23	24	25	26	27	28
Vojmån River															
Skikkisjaure	Dec. 48—Febr. 52	< 200	—	—	—	—	—	—	—	—	—	—	—	—	—
»	Dec. 48—Febr. 52	201—250	—	—	—	1	—	—	—	2	—	—	—	—	—
»	Dec. 48—Febr. 52	> 250	—	1	3	3	1	3	2	—	—	—	—	—	—
Dikasjön	Oct. 48—Dec. 51	< 200	—	—	—	—	—	—	—	—	—	—	—	—	—
»	Oct. 48—Dec. 51	201—250	—	—	—	—	1	1	1	1	1	—	—	1	—
»	Oct. 48—Dec. 51	> 250	—	—	—	—	—	1	5	4	11	8	6	5	1
»	Aug.—Sep. 55	—	—	—	1	2	—	3	3	7	15	24	20	13	20
Vojmsjön, north part ..	1948—1951	< 115	—	—	—	—	—	3	—	2	2	—	1	—	—
» » » ..	1948—1951	116—200	—	—	—	—	—	—	—	—	—	—	—	—	—
» » » ..	1948—1951	201—250	—	—	—	—	—	3	3	4	6	7	3	2	—
» » » ..	1948—1951	251—300	—	2	1	10	19	21	26	41	35	32	19	10	3
» » » ..	1948—1951	301—350	—	1	1	8	7	13	28	22	17	17	9	12	1
» » » ..	1948—1951	> 350	—	1	—	2	2	10	10	20	15	10	9	3	—
Vojmsjön, south part ..	1951—1955	115—200	—	—	—	—	—	—	—	—	—	—	—	—	—
» » » ..	1951—1955	201—250	—	—	—	—	—	—	—	—	—	—	—	—	—
» » » ..	1951—1955	251—300	—	—	1	2	3	3	2	1	2	1	—	—	—
» » » ..	1951—1955	301—350	—	—	—	1	4	3	2	2	—	1	2	—	—
» » » ..	1951—1955	> 350	—	—	1	3	6	4	2	1	—	—	1	—	—
» » » ..	1951—1955	—	3	10	23	53	91	107	87	81	56	28	22	19	14
Malgomaj	Aug. 51—Nov. 54	< 200	—	—	—	1	—	3	2	1	2	—	1	—	—
»	Aug. 51—Nov. 54	201—250	—	1	1	—	1	2	—	2	2	3	—	1	—
»	Aug. 51—Nov. 54	> 250	—	—	2	4	5	7	9	5	3	1	2	—	—
Volgsjön	Oct. 46—Nov. 56	< 200	—	—	—	—	1	3	5	3	1	—	—	—	1
»	Oct. 46—Nov. 56	201—250	—	—	—	3	2	2	1	—	—	—	1	—	—
»	Oct. 46—Nov. 56	> 251	—	1	—	—	—	4	5	7	4	1	—	—	—
Lomsjön (Rissjön)	Nov. 51	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Fjällsjöälven River															
Stora Arksjön	Jun.—Oct. 56	—	—	—	—	—	—	—	—	—	—	—	—	1	5
Nappsjön	Oct. 56	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Ormsjön	Nov. 46—Aug. 56	< 151	—	—	—	—	—	—	—	—	—	—	—	—	—
»	Nov. 46—Aug. 56	151—200	—	—	—	—	—	—	—	—	—	—	—	1	3
»	Nov. 46—Aug. 56	201—250	—	—	—	—	—	—	—	—	—	—	—	—	—
»	Nov. 46—Aug. 56	> 250	—	—	—	—	—	—	—	—	1	—	—	—	1
Tåsjön	Oct. 46—Aug. 56	< 200	—	—	—	—	—	—	—	—	—	—	—	—	—
»	Oct. 46—Aug. 56	> 200	—	—	—	—	—	—	—	—	—	—	—	—	—
»	Oct. 46—Aug. 56	—	—	—	—	—	—	—	—	—	—	—	—	1	5
Flåsjön	1946—1956	< 200	—	—	—	—	—	—	—	1	1	2	—	10	24
»	1946—1956	> 200	—	—	—	—	1	6	18	58	50	55	52	21	4
Faxälven River															
Sörvikssjön	Dec. 52	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Görvikssjön	Nov. 56	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Bågede	Nov. 52	—	—	—	—	—	—	—	—	—	—	—	1	1	2
Russfjärden	Oct. 51—Dec. 52	< 251	—	—	—	—	—	—	—	—	—	—	—	1	—
»	Oct. 51—Dec. 52	251—300	—	—	—	—	—	—	—	—	—	—	—	11	13
»	Oct. 51—Dec. 52	301—350	—	—	—	—	—	—	—	—	—	—	1	3	11
»	Oct. 51—Dec. 52	351—400	—	—	—	—	—	—	—	—	—	2	—	1	—
»	Oct. 51—Dec. 52	> 400	—	—	—	—	—	—	—	—	—	1	—	2	—
Fångsjön	May 53	< 251	—	—	—	—	—	—	—	—	—	—	3	5	4
»	May 53	251—300	—	—	—	—	—	—	—	—	—	2	2	7	2
»	May 53	301—350	—	—	—	—	—	—	—	—	—	—	1	3	5
»	May 53	> 350	—	—	—	—	—	—	—	—	—	—	—	1	2
»	Jun. 50—52	—	—	—	—	—	—	—	—	—	—	1	2	3	6
Sporrsjön	Jun. 50—52	—	—	—	—	—	—	—	—	—	1	3	3	17	39
Stamseleviken	Jul. 52	—	—	—	—	—	—	—	—	—	—	—	2	3	5
Sörsjön (Långsele)	May 54—Oct. 56	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mårdsjön	May—Dec. 53	—	—	—	—	1	2	—	—	—	—	—	—	1	3
Vängelvattnet	Jun.—Nov. 53	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Main river															
at the mouth	Oct. 75	—	—	—	—	—	—	—	—	—	—	—	—	1	1
» » »	Oct.—Dec. 55	—	—	—	—	—	—	—	1	—	1	3	4	10	20

the Ångermanälven River system.

29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	Sample	Mean
—	—	—	—	1	6	7	16	23	26	13	8	—	—	—	—	—	—	—	—	—	—	—	—	—	100	37.2
—	—	—	—	3	—	3	5	6	3	6	1	—	—	—	—	—	—	—	—	—	—	—	—	—	30	(36.8)
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13	19.6
—	—	1	3	—	2	8	17	19	27	21	25	19	13	7	2	1	1	—	—	—	—	—	—	—	166	38.8
—	—	1	1	5	2	3	3	5	5	12	6	5	6	2	1	—	1	1	—	—	—	—	—	—	65	—
—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	43	(24.7)
7	5	1	2	3	4	2	5	10	9	11	5	2	5	4	1	4	4	3	3	2	1	—	—	—	201	—
—	—	—	1	—	1	3	7	9	5	9	7	5	—	1	—	1	—	—	—	1	—	—	—	—	58	—
—	1	—	—	—	1	2	3	4	1	2	1	1	—	—	—	—	—	—	—	—	—	—	—	—	16	36.7
2	2	3	2	1	—	1	—	2	2	—	1	2	—	—	1	1	—	—	—	1	—	—	—	—	49	—
13	1	—	1	1	—	—	1	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	238	(23.6)
3	3	—	1	—	—	—	1	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	156	(22.9)
2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	85	(23.4)
—	—	—	—	—	—	—	—	—	—	1	1	7	8	9	22	25	15	13	10	5	—	3	—	—	119	45.1
—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	1	3	2	3	—	1	—	—	—	12	46.4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	4	2	—	1	—	—	—	—	—	26	(21.3) (45.1)
—	—	—	—	1	—	—	—	—	—	—	—	—	—	1	1	—	—	—	2	2	—	—	—	—	22	(21.9) (46.8)
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	18	20.7
6	—	—	1	1	—	—	1	—	—	1	2	13	15	32	42	51	64	50	33	32	7	3	1	—	949	—
1	1	—	1	2	3	8	8	9	11	10	10	3	5	1	—	—	—	—	—	—	—	—	—	—	83	(—) (37.8)
—	1	—	1	2	1	1	4	5	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	31	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	38	21.6
2	1	5	14	25	25	61	83	79	54	30	21	7	1	—	—	—	—	—	—	—	—	—	—	—	422	(22.0) (36.3)
—	—	—	—	1	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12	—
—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23	(22.4)
1	1	2	5	7	15	23	17	11	11	6	2	1	—	—	—	—	—	—	—	—	—	—	—	—	102	35.5
7	16	13	30	23	16	18	10	6	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	146	32.7
1	6	17	12	27	30	12	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	114	33.0
1	1	4	4	12	10	16	26	19	18	20	12	8	4	—	1	—	—	—	—	—	—	—	—	—	156	36.7
6	11	10	18	18	9	8	10	3	4	6	9	—	1	1	—	—	—	—	—	—	—	—	—	—	118	33.8
4	2	6	7	9	11	9	5	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	56	33.3
—	1	5	1	1	4	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	17	32.0
4	6	3	6	11	9	8	5	3	2	2	1	2	—	4	2	1	—	—	—	—	—	—	—	—	69	34.8
4	4	5	9	7	5	6	2	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	43	32.7
4	2	9	17	11	19	30	18	28	17	29	26	19	19	18	9	3	1	1	—	—	—	—	—	—	286	—
27	38	33	25	15	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	179	30.1
2	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	270	24.6
—	1	—	—	1	1	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	33.8
4	8	12	12	9	14	13	9	6	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	92	33.2
2	4	5	4	3	1	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	26	31.1
4	2	3	9	7	11	26	29	21	17	8	3	2	—	—	—	—	—	—	—	—	—	—	—	—	143	35.5
12	14	26	31	22	26	21	23	12	11	7	3	—	—	—	—	—	—	—	—	—	—	—	—	—	232	33.0
5	19	16	18	14	10	6	10	5	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	121	32.0
3	1	6	7	5	4	6	2	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	39	32.4
—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—
1	2	1	6	5	2	3	1	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	37	31.4
7	6	6	5	3	4	1	2	3	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	53	31.0
2	2	7	5	—	2	2	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	31	30.7
2	4	—	3	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	14	30.4
14	23	12	10	1	—	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	78	30.2
35	31	49	28	26	13	9	2	5	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	263	30.6
10	5	8	5	3	—	—	—	—	1	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	44	30.4
—	—	4	7	4	6	6	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	27	33.7
4	1	11	9	11	15	4	5	2	1	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	72	(19.7) (32.9)
1	9	18	21	25	41	21	15	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	157	33.4
1	1	3	—	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	30.9
22	28	26	33	19	12	6	—	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	189	30.6

Total: 6.169 specimens

Table 9. Whitefish samples from

Lake, locality	Date	Size	15	16	17	18	19	20	21	22	23	24	25	26
Helgesjön	Nov. 55—Dec. 56	< 250	—	—	—	—	—	—	—	—	—	—	—	1
»	Nov. 55—Dec. 56	251—350	—	—	—	—	—	1	1	—	—	3	1	3
»	Nov. 55—Dec. 56	351—400	—	—	—	—	—	—	1	4	2	2	2	—
»	Nov. 55—Dec. 56	> 400	—	—	—	1	—	1	1	5	1	1	3	2
Kallsjön	Nov. 50—56	—	—	—	—	—	—	1	1	8	15	29	53	47
Sällsjön	Nov. 53	—	—	—	—	—	—	—	1	2	2	10	16	21
Stamsjön	May 57	—	—	—	—	—	—	—	—	—	1	1	—	2
Dammån	Aug. 50	—	—	—	—	—	5	4	6	6	3	1	—	—
Ockesjön	Nov. 50—Dec. 52	—	—	—	—	—	1	1	2	8	6	14	12	11
Kvitsleströmmen, north	Oct. 53	—	—	—	—	—	1	2	4	7	7	18	12	12
» south	Nov. 51	—	—	—	1	—	3	2	15	10	7	8	1	—
Storsjön	1950—1954	< 200	—	—	—	—	2	—	2	3	3	5	6	9
»	1950—1954	201—300	—	—	—	1	2	5	8	11	24	30	30	27
»	1950—1954	301—400	—	—	—	2	6	5	8	21	10	12	6	9
»	1950—1954	> 400	—	—	—	1	1	—	2	2	4	4	—	1
Näckten	Jan. 49	< 170	—	—	—	—	—	—	—	—	—	—	—	—
»	Dec. 48	> 350	—	—	—	—	—	6	10	2	2	2	—	—
Nästån[1] river	Sep. 50—Nov. 53	—	—	—	—	—	—	2	11	17	38	76	78	85
Nälden	Oct.—Dec. 48	< 250	—	—	—	—	—	—	—	1	—	1	—	1
»	Oct.—Dec. 48	251—350	—	—	—	—	2	6	8	2	1	1	—	—
»	Oct.—Dec. 48	> 350	—	—	—	—	—	5	4	6	1	1	—	—
Alsen	Dec. 54—Mar. 56	< 250	—	—	—	—	—	—	—	—	1	—	—	1
»	Dec. 54—Mar. 56	> 250	—	—	—	—	3	3	—	3	—	—	2	3
Långan River														
Yttre Oldsjön	Oct. 56	—	—	—	—	—	—	—	2	3	8	13	21	24
Rönnösjön	Jul. 45—Nov. 51	—	—	—	—	—	—	—	—	—	2	4	1	8
Landösjön	Sep. 44—Nov. 54	< 170	—	—	—	—	—	—	—	—	—	—	—	—
»	Jul.—Aug. 45	> 250	—	—	—	—	—	—	—	—	—	—	3	4
»	Nov. 50—Dec. 51	> 250	—	—	—	—	—	1	—	—	—	1	5	6
Hårkan River														
Valsjön	1948—1955	—	—	—	—	—	—	—	—	—	—	—	—	—
Hotagen	Nov. 55	< 200	—	—	—	—	—	—	—	—	—	—	—	—
»	Nov. 55	> 200	—	—	—	—	—	—	—	—	1	—	—	—
Häggsjön	1948—1955	—	—	—	—	—	—	—	—	—	—	—	—	—
Lövsjön	Dec. 54—55	< 150	—	—	—	—	—	—	—	—	—	—	—	—
»	Dec. 54	> 150	—	—	—	—	—	—	—	—	—	—	—	—
Sandvikssjön	Nov. 54	< 170	—	—	—	—	—	—	—	—	1	—	3	8
»	Nov. 51—54	> 200	—	—	—	—	—	—	—	1	7	13	15	21
Midskogsmagasinet	Jan. 56	—	—	—	—	—	1	—	11	12	29	25	24	19
Skellbrejden	Jan. 56	—	—	—	—	—	—	—	—	—	—	—	—	—
Sittsjön	Aug. 51	—	—	—	—	—	—	—	—	—	—	—	—	—
Gesunden[2]	Nov. 51—52	< 250	—	—	—	—	1	—	—	—	—	—	2	2
»[2]	Nov. 51—52	> 250	—	—	—	—	—	—	—	1	2	2	3	2
Ammerån River														
Öjarn	Jul. 55	—	—	—	—	—	—	—	—	—	—	—	1	—
Ottsjön	Nov. 53—Jan. 53	< 250	—	—	—	—	—	1	1	—	—	—	—	—
»	Nov. 53—Jan. 55	> 250	1	5	8	11	15	12	9	6	1	2	—	1
Gåxsjön	Jan. 55—Nov. 56	< 250	—	1	—	1	4	1	—	—	—	—	—	1
»	Jan. 55—Nov. 56	> 250	—	1	1	5	1	3	1	—	—	1	—	2
Hammerdalssjön	Nov. 56	—	—	—	—	2	3	6	2	2	1	1	—	1
Gillerån River														
Fullsjön	Dec. 55	—	—	—	—	—	—	—	—	—	—	—	—	—
Hammarforsmagasinet[2]	Sep.—Oct. 56	—	—	—	—	—	—	—	1	5	9	9	13	13
Indalsälven, mouth	Nov. 50	—	—	—	—	—	—	—	—	—	—	—	—	—

[1] Details of the samples from the Nästån in table 9 a—c.

[2] Includes the samples published by LINDROTH (1957).

the Indalsälven River system.

27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	Sample	Mean
—	1	—	—	1	—	2	4	3	5	5	11	8	9	5	7	3	—	—	—	—	—	65	38.1
2	5	1	6	1	6	2	4	10	12	7	16	7	5	4	5	2	1	—	—	—	—	105	35.0
1	1	1	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	25.1
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	23.1
27	25	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	212	25.5
17	19	5	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	95	26.3
3	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	26.3
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	25	21.0
7	4	6	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	76	25.2
8	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	73	24.3
2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	49	22.1
7	7	7	6	7	5	5	16	18	32	32	34	23	14	13	4	2	—	—	—	—	—	262	34.6
22	14	11	19	18	27	40	47	67	88	91	110	107	67	30	14	6	2	—	—	—	—	918	34.4
6	4	6	1	2	2	3	—	—	1	1	3	—	1	—	—	—	—	—	—	—	—	109	24.9
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15	22.5
—	—	—	—	1	—	—	1	2	4	14	33	22	20	12	7	4	—	—	—	—	—	120	38.9
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	22	21.3
98	110	112	126	168	161	164	102	88	53	29	14	3	5	1	1	—	—	—	—	—	—	1.378	—
2	2	3	4	7	9	6	5	8	5	2	4	1	2	1	—	—	—	—	—	—	—	64	32.9
1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	22	21.5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	17	21.4
5	5	10	9	4	4	2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	44	29.6
1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	22.9
16	6	6	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	101	25.6
6	7	5	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	36	26.9
—	—	2	5	1	3	4	1	2	—	1	—	—	1	—	—	—	—	—	—	—	—	20	32.4
—	2	3	4	2	—	3	1	1	1	1	—	1	—	—	—	—	—	—	—	—	—	26	30.2
2	2	5	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	25	26.8
—	—	—	—	—	—	—	—	1	2	15	31	66	75	68	56	36	12	5	—	1	1	369	40.5
—	—	—	—	—	3	5	9	11	12	7	2	—	1	—	—	—	—	—	—	—	—	50	35.2
1	1	1	—	3	1	6	1	1	9	13	30	36	57	52	29	12	5	3	2	—	—	264	39.5
5	19	42	60	70	49	33	17	6	1	3	—	—	1	1	—	—	—	—	—	—	—	307	31.0
—	—	—	—	1	6	8	28	23	19	9	9	3	1	—	—	—	—	—	—	—	—	107	35.1
—	—	—	—	1	1	3	6	13	21	22	18	13	9	3	2	1	—	—	—	—	—	113	37.1
14	26	26	24	13	2	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	120	28.8
38	51	33	21	14	7	6	1	4	7	3	1	1	2	—	—	—	—	—	—	—	—	246	28.5
15	10	7	7	4	4	4	2	—	3	—	—	1	—	—	—	—	—	—	—	—	—	178	25.7
—	—	—	—	—	1	4	11	15	25	20	7	2	4	1	—	1	—	—	—	—	—	91	36.2
1	2	—	1	2	—	1	1	1	—	2	2	2	3	1	1	—	—	—	—	—	—	20	35.4
6	5	20	19	11	12	6	1	1	1	1	—	1	—	—	—	—	—	—	—	—	—	89	30.1
2	—	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15	25.7
—	—	—	4	4	11	16	11	12	13	7	2	2	2	—	—	—	—	—	—	—	—	85	34.2
1	—	1	1	—	—	2	1	3	8	9	14	26	20	20	11	8	6	—	1	1	—	135	39.1
—	—	—	—	1	—	—	—	—	—	—	—	1	1	—	1	—	—	—	—	—	—	75	(19.3)
3	2	4	2	1	—	3	5	11	11	23	25	32	18	21	5	4	1	—	—	—	—	179	36.9
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15	19.9
1	1	1	1	2	1	—	4	4	3	4	4	3	1	—	—	—	—	—	—	—	—	48	—
—	—	—	—	2	—	2	2	2	6	3	2	—	—	—	—	—	—	—	—	—	—	19	35.2
5	8	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	65	25.2
—	3	7	8	8	8	10	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	50	31.3

Total: 6.575 specimens

Table 9 a. Samples of whitefish, spawning at Nästån River in the year 1951.

Day	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Oct. 5	—	—	1	3	1	2	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8	—	—	1	—	—	3	2	—	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—
9	—	—	—	2	3	1	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
11	—	1	—	—	3	1	1	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—
13	—	—	1	—	4	3	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
20	—	—	1	2	1	—	2	3	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—
22	—	—	1	2	2	2	—	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
24	—	—	2	—	1	2	2	1	—	2	1	2	—	—	—	—	1	—	—	—	—	—	—
26	—	1	—	1	2	4	4	2	1	1	1	—	1	1	1	—	—	—	—	—	—	—	—
28	—	—	—	1	4	1	2	2	2	3	1	—	—	1	—	—	—	—	—	—	—	—	—
30	—	1	—	—	—	1	3	1	2	—	—	2	1	1	1	—	1	1	—	—	—	—	—
Nov. 1	—	—	—	1	—	3	—	3	1	2	2	—	1	1	—	1	1	—	—	—	—	—	—
3	—	—	—	—	2	1	1	2	—	1	1	1	—	—	1	—	—	—	—	—	—	—	—
5	—	—	—	—	—	—	—	—	3	2	2	2	3	4	1	1	—	—	—	—	—	—	—
7	—	—	—	—	—	—	1	—	1	—	4	3	2	1	2	2	1	—	1	—	—	—	—
9	—	—	—	1	—	—	—	1	2	4	—	2	3	5	—	1	—	—	1	—	—	—	—
11	—	—	—	1	—	—	—	—	—	1	—	7	2	3	3	1	1	—	—	—	1	—	—
13	—	—	—	—	—	—	—	1	2	—	2	3	1	3	4	2	1	1	—	—	—	—	—
15	—	—	—	—	—	—	1	1	4	1	1	1	1	4	2	1	—	—	—	—	—	—	—
17	—	—	—	—	2	—	—	1	1	—	—	3	4	3	2	—	3	1	—	—	—	—	—
19	—	—	—	—	—	—	—	—	—	2	1	3	5	2	4	1	2	—	—	—	—	—	—
21	—	—	—	—	—	1	—	—	1	—	1	2	2	5	3	1	3	1	—	—	—	—	—
23	—	—	—	—	—	—	—	—	1	—	4	—	5	4	3	3	—	—	—	—	—	—	—
25	—	—	—	—	—	—	1	1	—	—	—	—	3	2	1	4	6	—	1	1	—	—	—
29	—	—	—	—	—	—	—	—	—	—	1	1	1	2	—	—	—	—	—	—	1	—	—

Table 9 b. Samples of whitefish, spawning at Nästån River in the year 1952.

Day	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Oct. 8	—	—	—	1	2	4	2	4	4	1	1	—	—	1	—	—	—	—	—	—	—	—	—
10	—	—	—	—	3	6	2	5	2	1	1	—	—	—	—	—	—	—	—	—	—	—	—
12	—	—	1	—	3	1	2	4	4	2	1	2	—	—	—	—	—	—	—	—	—	—	—
14	—	—	—	2	5	3	4	—	1	3	1	1	—	—	—	—	—	—	—	—	—	—	—
16	—	1	1	—	—	2	3	2	1	3	2	1	—	2	—	—	1	—	—	—	—	—	—
18	—	—	1	1	1	1	2	3	2	1	—	2	4	—	1	—	1	—	—	—	—	—	—
20	—	—	—	1	1	2	—	2	4	1	4	4	—	—	—	—	1	—	—	—	—	—	—
22	—	—	—	1	2	3	—	1	1	5	—	2	3	—	1	1	—	—	—	—	—	—	—
24	—	—	—	1	—	—	—	1	—	—	2	4	3	4	2	2	—	1	—	—	—	—	—
26	—	—	—	—	—	—	1	1	1	1	3	2	2	3	—	2	1	2	1	—	—	—	—
28	—	—	—	—	—	—	1	—	—	1	2	6	2	3	1	3	—	—	—	—	—	—	—
30	—	—	—	—	—	—	—	1	1	1	2	2	7	—	2	—	4	—	—	—	—	—	—
Nov. 1	—	—	—	—	—	—	—	1	3	—	1	1	2	1	2	3	1	2	—	—	—	—	—
3	—	—	—	—	—	—	—	1	2	2	4	1	1	5	2	1	1	—	—	—	—	—	—
5	—	—	—	—	—	—	—	1	3	2	3	1	2	4	2	1	—	1	—	—	—	—	—
7	—	—	—	—	—	1	—	1	—	2	3	1	3	4	2	2	—	1	—	—	—	—	—
9	—	—	—	—	—	—	1	1	2	3	1	3	3	2	—	—	2	1	—	—	—	—	—
11	—	—	—	—	—	—	—	—	2	3	3	2	1	4	2	1	—	—	—	—	—	—	—
13	—	—	—	—	—	—	1	—	—	2	4	3	4	2	1	2	—	—	—	—	1	—	—
15	—	—	—	—	—	—	—	1	—	2	5	3	3	4	—	1	1	—	—	—	—	—	—
17	—	—	—	—	1	—	—	—	2	2	1	3	1	2	4	2	1	—	—	—	—	—	—
19	—	—	—	—	1	—	—	—	1	—	1	1	5	4	1	2	3	—	1	—	—	—	—
21	—	—	—	—	—	—	—	—	2	2	2	3	2	1	1	1	—	—	—	—	—	—	—
23	—	—	—	—	—	—	—	—	1	1	1	3	3	2	1	1	—	1	—	—	—	—	—
25	—	—	—	—	—	—	—	—	1	—	2	2	2	6	1	2	—	—	—	—	—	1	—
27	—	—	—	—	—	—	2	1	1	1	1	2	3	3	—	1	1	2	1	—	—	—	—

Table 9 c. Samples of whitefish, spawning at Nästån River in the year 1953.

Day	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Sep. 26	1	1	—	—	1	1	5	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
28	—	—	1	—	1	3	3	3	1	1	1	—	—	2	—	—	—	—	—	—	—	—	—
30	—	—	—	4	6	2	1	2	—	2	1	—	—	1	—	—	—	—	1	—	—	—	—
Oct. 2	—	—	1	2	1	1	5	1	3	1	—	2	1	1	—	1	—	—	—	—	—	—	—
4	—	1	1	3	1	4	2	—	2	—	1	—	—	2	1	—	—	2	—	—	—	—	—
6	—	1	—	—	2	1	—	2	3	2	2	2	—	—	5	—	—	—	—	—	—	—	—
8	—	—	—	2	5	5	3	3	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—
10	—	1	—	3	2	2	2	2	3	1	1	1	1	—	—	—	—	—	—	—	—	—	—
14	—	—	1	—	1	—	3	4	—	3	2	3	3	—	—	—	—	—	—	—	—	—	—
16	—	—	2	—	2	2	2	1	—	2	3	2	1	2	—	1	—	—	—	—	—	—	—
18	—	—	—	1	1	1	3	4	2	2	1	1	2	1	—	1	—	—	—	—	—	—	—
20	—	—	—	—	3	1	2	1	1	1	3	1	2	1	1	—	—	1	—	—	—	—	—
22	—	—	—	—	1	1	2	—	1	2	2	2	3	4	—	—	2	—	—	—	—	—	—
24	—	—	—	—	—	1	2	2	1	5	1	2	1	1	1	—	1	2	—	—	—	—	—
26	—	—	—	—	—	—	—	1	1	1	1	5	3	4	1	2	—	1	—	—	—	—	—
28	—	—	—	—	—	—	—	—	1	1	3	4	3	1	4	1	—	—	1	1	—	—	—
30	—	—	—	—	—	—	2	—	2	3	2	3	3	1	2	2	—	—	—	—	—	—	—
Nov. 1	—	—	—	—	—	—	—	—	3	4	—	2	2	5	2	—	1	—	1	—	—	—	—
3	—	—	—	—	—	—	—	—	—	1	4	6	2	2	2	2	—	1	—	—	—	—	—
5	—	—	—	—	—	1	—	1	1	2	3	3	2	1	4	2	—	—	—	—	—	—	—
7	—	—	—	—	—	—	—	1	—	2	1	2	6	2	2	2	1	1	—	—	—	—	—
9	—	—	—	—	—	—	1	1	1	1	4	2	6	2	—	—	1	1	—	—	—	—	—
11	—	—	—	—	—	—	—	1	1	2	2	3	—	2	2	2	—	—	—	1	1	—	—
13	—	—	—	—	—	—	—	—	1	2	—	2	4	2	4	3	—	1	—	—	—	—	—
15	—	—	—	—	—	—	1	—	1	—	—	7	3	2	4	1	—	—	1	—	—	—	—
17	—	—	—	—	—	—	—	—	1	1	1	4	4	6	—	1	—	1	1	—	—	—	—
19	—	—	—	—	—	—	—	2	—	—	3	4	2	2	3	1	2	—	1	—	—	—	—
21	—	—	—	—	—	—	—	—	—	2	3	1	2	1	—	2	—	1	1	—	—	—	—
23	—	—	—	—	—	—	—	1	—	1	2	3	3	1	2	2	2	—	1	—	1	—	1
25	—	—	—	—	—	—	—	1	1	—	2	—	2	7	—	2	2	1	—	—	—	—	—

Table 10. Whitefish samples

Lake, locality	Date	Size	16	17	18	19	20	21	22	23	24	25	26
Storsjön	1948—1954	< 300	—	—	1	1	2	2	—	1	—	1	—
»	1948—1954	> 300	—	3	7	12	25	34	20	16	4	1	—
Klövsjön	Jan. 53	—	—	—	—	—	—	—	—	—	—	—	—
Hålen	Dec. 51—Jan. 53	—	—	—	—	—	—	—	—	—	1	—	—
Rätanssjön	Dec. 51	—	—	—	—	—	—	—	—	—	—	—	—
Rätan-Holmsjön	1948—1955	—	1	1	3	2	4	2	2	2	3	4	2
Holmsjön	1948—1955	< 300	—	—	1	1	2	—	—	—	—	—	—
»	1948—1955	> 300	1	5	6	15	16	11	15	4	3	3	1
Gimån River													
Noren	Dec. 55	—	—	—	—	—	—	—	—	—	—	—	—
Pån	Dec. 55	—	—	—	—	—	—	—	—	—	—	—	—
Bodsjön	Dec. 55	< 250	—	—	—	—	—	—	—	—	—	—	1
»	Dec. 55	> 250	—	—	1	—	3	1	1	1	—	—	—
Hungesjön	Jan. 56	—	—	—	—	—	—	—	—	—	—	1	1
Locknesjön	Oct. 56—Feb. 57	—	—	1	4	14	19	26	26	25	16	7	2
Bensjön	Jan. 57	—	—	—	—	—	—	—	—	—	—	—	—
Revsundssjön	Dec. 51—55	—	—	—	—	—	—	—	—	—	—	—	—
Hållstasjön	Dec. 51—Feb. 52	—	—	—	—	—	—	—	—	—	—	—	—
Sundsjön	Jan. 51	< 250	—	—	—	—	—	—	—	—	—	—	—
»	Jan. 51	> 250	—	—	1	—	2	2	3	2	4	1	1
Idsjön	1947—1957	< 200	—	—	—	2	1	16	44	112	193	296	286
»	1947—1957	201—350	—	—	3	3	5	3	3	1	1	—	—
»	1947—1957	> 350	2	9	17	25	43	40	16	7	5	3	4
Skåsjön	Jan. 57	—	—	—	—	—	—	—	—	—	—	—	—
Röringen	Dec. 55	—	—	—	—	—	—	—	—	—	—	—	—
Öfsjön	Jan. 56—57	< 250	—	—	—	—	—	—	—	—	—	—	—
»	Jan. 56—57	251—300	—	—	—	—	—	—	—	—	—	—	—
»	Jan. 56—57	301—350	—	—	—	—	—	—	—	—	—	—	—
»	Jan. 56—57	> 350	—	—	—	—	—	—	—	—	—	—	—
Sicksjön	Nov. 49—Feb. 56	< 200	—	—	—	—	—	—	—	—	—	—	—
»	Nov. 49—Feb. 56	201—250	—	—	—	—	—	—	1	—	—	—	—
»	Nov. 49—Feb. 56	251—300	—	—	—	—	3	1	2	3	3	—	2
»	Nov. 49—Feb. 56	301—350	—	—	1	2	5	8	15	19	13	9	4
»	Nov. 49—Feb. 56	> 350	—	—	1	2	5	15	12	13	16	9	8
Ansjön	Dec. 51—Feb. 56	< 200	—	—	—	—	—	—	—	—	—	—	—
»	Dec. 51—Feb. 56	201—250	—	—	—	—	—	—	—	—	—	—	—
»	Dec. 51—Feb. 56	251—300	—	—	—	—	—	1	—	—	—	1	—
»	Dec. 51—Feb. 56	301—350	—	—	—	—	—	—	—	—	—	—	—
»	Dec. 51—Feb. 56	> 350	—	—	—	—	—	—	—	—	—	—	—
Holmsjön	Nov. 47—48	—	—	—	—	—	—	—	1	—	4	5	3
Navarn	Dec. 55	—	—	—	1	—	2	4	4	2	2	—	—
Ljungan,[1] at the mouth	Sep. 51—52	—	—	—	—	—	—	—	—	—	—	—	1

---

[1] From LINDROTH (1957).

from the Ljungan River system.

27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	Sample	Mean
—	—	—	1	2	1	9	17	29	42	38	47	21	11	3	—	—	—	—	—	—	—	299	(36.7)
—	—	—	—	—	—	—	1	—	1	—	—	—	—	1	—	—	—	—	—	—	—	125	(20.9)
—	—	—	—	1	3	13	23	23	18	11	9	4	1	—	—	—	—	—	—	—	—	106	35.2
—	—	—	2	2	6	12	22	32	25	16	5	2	3	—	—	—	—	—	—	—	—	128	35.0
—	—	—	—	1	6	8	14	19	18	17	8	5	1	—	—	—	—	—	—	—	—	97	35.5
6	2	5	7	5	8	2	3	5	4	—	—	—	—	—	—	—	—	—	—	—	—	73	—
1	—	2	2	5	8	4	13	22	25	34	27	28	11	4	8	5	2	1	1	—	—	207	(37.0)
—	—	—	1	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	84	(20.5)
—	—	—	—	—	—	2	7	7	19	17	16	6	5	1	1	1	—	—	—	—	—	82	37.0
1	2	8	8	12	17	14	14	14	8	6	2	1	1	—	—	—	—	—	—	—	—	108	33.0
1	5	8	12	8	10	8	6	2	—	—	—	—	—	—	—	—	—	—	—	—	—	61	31.0
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	20.6
3	7	8	6	15	12	11	9	4	3	2	1	—	—	—	—	—	—	—	—	—	—	83	31.5
2	1	—	—	1	1	—	—	—	—	4	3	16	22	15	18	18	15	8	1	—	1	266	(21.8) (41.5)
—	—	1	2	8	8	14	13	8	6	1	3	—	—	—	—	—	—	—	—	—	—	64	33.5
—	—	—	—	3	5	5	13	19	29	32	33	15	7	1	3	2	—	—	—	—	—	167	36.7
—	—	—	—	—	—	1	2	2	4	2	3	1	2	—	—	—	—	—	—	—	—	17	36.6
—	—	—	—	—	2	2	2	4	10	9	7	6	4	1	3	—	—	—	—	—	—	50	37.2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	22.4
220	140	69	40	20	10	3	3	2	2	2	—	—	—	—	—	—	—	—	—	—	—	1.461	25.9
—	—	3	3	12	35	61	95	110	137	134	91	66	28	18	6	1	—	—	—	—	—	819	(20.4) (36.0)
1	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	174	(20.4)
—	—	—	—	1	—	—	2	13	18	22	27	13	4	5	4	—	—	—	—	—	—	109	37.4
—	—	1	1	6	9	13	15	8	9	7	3	2	1	—	2	—	—	—	—	—	—	77	34.5
—	—	—	—	—	—	—	1	2	6	7	14	21	29	30	36	20	14	5	4	2	—	191	40.9
—	—	—	—	—	—	—	—	1	2	4	3	7	12	12	7	8	4	4	1	1	1	67	41.0
—	—	—	—	—	—	—	2	3	2	6	6	11	14	4	11	7	3	2	—	—	—	71	39.9
—	—	—	—	—	—	—	—	1	2	5	15	14	14	11	5	4	—	—	—	—	—	71	39.5
1	4	8	20	31	33	38	30	40	27	14	11	2	3	1	3	2	1	—	1	—	—	270	33.7
2	5	8	23	36	37	55	57	53	40	24	19	14	8	11	5	5	5	3	—	1	—	412	34.6
1	1	—	—	—	—	1	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	16	—
2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	78	22.9
—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	83	23.0
—	—	—	1	4	17	24	33	54	69	72	48	37	12	9	4	1	1	—	—	—	—	386	36.3
—	2	1	8	12	16	34	49	54	43	30	36	20	12	3	—	—	—	—	—	—	—	320	35.3
—	1	4	10	19	25	47	39	43	32	18	2	4	1	—	—	—	—	—	—	—	—	247	33.8
1	—	4	2	5	5	6	12	11	5	4	1	1	1	—	—	—	—	—	—	—	—	58	33.7
—	—	—	—	—	1	2	3	2	—	2	2	1	1	—	—	—	—	—	—	—	—	14	35.6
5	4	9	14	16	8	3	2	1	2	—	—	—	—	—	—	—	—	—	—	—	—	77	29.5
—	—	—	—	—	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	17	(21.6)
4	5	19	17	20	18	10	13	3	—	—	—	—	—	—	—	—	—	—	—	—	—	110	31.0

Total: 7.098 specimens

Table 11. Whitefish samples from the

Lake, locality	Date	Size	18	19	20	21	22	23	24	25	26	27
Delångersån River												
Hångstaörn	Jun. 56	—	—	—	—	—	—	—	—	—	—	—
Dellen	Nov. 49—55	—	1	2	1	5	4	12	12	7	6	3
Ljusnan River												
Östra Vattnan	Jan. 53	—	—	—	2	4	6	12	11	2	3	—
Västra Vattnan	Dec. 52	—	—	—	—	—	—	1	2	4	10	3
Myskelån	Sep. 56	—	—	—	—	—	—	—	—	—	—	1
Lill-Ljusnan	May 53—Oct. 56	—	—	—	—	—	3	3	6	11	20	45
Lossnen	May 52—Nov. 54	< 200	—	—	—	—	—	1	—	3	1	2
»	May 52—Nov. 54	201—250	—	—	—	—	—	1	—	2	9	10
»	May 52—Nov. 54	> 250	—	—	—	—	—	1	2	7	22	42
Ulften	Aug. 56	—	—	—	—	—	3	1	5	14	15	24
Nedre Särvsjön	Oct. 55	—	—	1	—	—	—	—	1	—	—	1
Vikarsjön	Jun.—Oct. 56	< 200	—	—	—	—	—	1	1	1	1	1
	Jun.—Oct. 56	> 200	—	—	—	—	—	2	4	4	4	6
Orrmosjön	Oct. 55—Nov. 56	< 200	—	—	—	—	—	—	—	—	—	—
»	Oct. 55—Nov. 56	201—250	—	—	—	—	—	1	—	1	—	—
»	Oct. 55—Nov. 56	> 250	—	—	4	2	5	5	6	6	3	2
Linsällsjön	Oct. 56	—	—	—	—	—	—	—	—	—	1	—
Målingen	Sep. 55	—	—	—	—	—	—	—	—	—	—	—
Öjingen	Oct. 55	—	—	—	—	—	—	—	—	—	—	—
Voxnan River												
Tandsjön	Nov. 51—53	—	—	—	4	6	9	16	23	18	19	16
Fågelsjön	Oct. 56	—	—	—	—	—	—	—	—	—	1	—
Öjungen	Nov. 49	—	—	2	1	6	8	8	7	5	2	—

Delångersån and the Ljusnan River system.

28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	Sample	Mean
—	—	—	—	—	1	—	4	8	3	11	9	2	—	1	—	—	—	39	37.5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	55	23.5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	40	23.1
2	4	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	31	26.9
3	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	28.6
53	56	53	37	19	14	4	—	—	—	—	—	—	—	—	—	—	—	324	28.8
11	18	32	47	56	71	35	23	11	2	—	—	—	—	—	—	—	—	313	32.0
13	10	12	5	6	1	—	1	—	—	—	—	—	—	—	—	—	—	70	28.7
52	62	52	26	17	9	2	1	—	—	1	—	—	—	—	—	—	—	296	28.9
22	10	6	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	105	27.0
—	2	—	—	2	1	4	2	4	5	1	1	—	—	—	—	—	—	25	(35.5)
1	1	7	13	31	37	57	32	29	25	19	3	—	—	—	—	—	—	260	34.1
2	2	1	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	27	26.6
—	—	—	—	—	—	—	—	2	5	3	4	4	5	3	—	—	—	26	39.2
—	—	—	—	—	—	—	—	—	—	3	5	3	3	2	2	1	2	21	40.8
—	1	—	—	—	—	1	—	—	1	—	—	—	—	1	—	1	—	38	23.6
—	3	4	3	9	5	3	2	2	2	1	1	1	—	—	1	—	—	38	33.1
—	—	—	—	2	2	2	4	10	4	1	—	1	1	—	—	—	—	27	35.7
—	—	—	—	4	6	1	1	1	2	1	2	1	4	2	—	—	—	25	36.4
11	11	11	7	6	3	3	4	1	4	1	—	—	—	1	—	—	—	174	—
2	3	3	7	4	5	1	2	—	—	—	—	—	—	—	—	—	—	28	31.2
—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	40	23.0

Total: 2.008 specimens

Table 12. Whitefish samples from

Lake, locality	Date	Size	17	18	19	20	21	22	23	24	25	26
Österdalälven River												
Idresjön	Jun. 51—Oct. 53	< 299	—	—	2	2	1	3	1	4	8	11
»	Jun. 51—Oct. 53	> 299	—	1	—	—	2	—	1	3	3	1
Särnasjön	Jun. 51—Oct. 54	—	1	—	2	1	2	4	4	4	8	15
Garberg	Jun. 53	—	—	1	1	—	4	1	1	2	—	2
Aldersäng	Nov. 51—54	< 300	—	—	—	—	—	—	1	—	1	—
»	Nov. 51—54	301—350	—	—	—	—	—	—	—	—	1	1
»	Nov. 51—54	351—400	—	—	—	4	2	4	3	1	3	—
»	Nov. 51—54	> 400	1	—	4	7	10	16	5	6	—	—
Stora Kölsjön	Oct. 55—56	—	—	—	—	—	—	—	—	1	—	3
Skattungen	Nov. 51	—	—	—	—	—	—	—	—	—	—	—
Siljan	Aug. 48—Dec. 54	< 250	—	—	—	—	—	—	1	—	—	1
»	Aug. 48—Dec. 54	251—300	—	—	—	—	—	—	2	—	2	6
»	Aug. 48—Dec. 54	301—350	—	—	2	2	1	1	2	—	2	5
»	Aug. 48—Dec. 54	351—400	—	2	4	4	2	3	4	4	1	8
»	Aug. 48—Dec. 54	> 400	1	—	2	1	5	1	2	1	7	7
Västerdalälven River												
Horrmundsjön	Jun. 54—Sep. 56	—	—	—	—	—	—	—	—	—	—	1
Öjesjön	Oct. 52—Jan. 54	—	—	—	—	—	—	—	1	—	—	—
Venjan	Oct. 51—Nov. 52	< 200	—	—	—	—	—	—	—	—	—	—
»	Oct. 51—Nov. 52	> 200	—	—	—	—	—	—	—	—	—	—
Van	Oct. 52	—	—	—	—	—	—	—	—	—	—	—
Amungen	Oct. 54—Nov. 56	—	—	—	—	—	—	—	—	—	—	—
Ljugaren	Nov.—Dec. 51	—	—	—	—	—	—	1	1	1	7	8
Rogsjön	Nov. 51	—	—	—	—	—	—	—	—	—	—	—
At the mouth	Nov. 56	—	—	—	—	—	—	—	—	—	—	6

the Dalälven River system.

27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	Sample	Mean
9	11	14	4	1	1	2	2	—	1	—	—	—	—	—	—	—	—	77	27.0
2	2	1	3	—	1	—	—	—	—	—	—	—	—	—	—	—	—	20	25.9
33	29	36	31	31	22	9	6	2	—	1	1	—	1	—	—	1	1	245	29.0
1	—	—	2	2	—	2	—	—	—	2	—	—	1	—	—	—	—	22	27.0
—	1	—	2	2	2	5	4	5	5	5	2	1	1	—	—	—	—	37	34.0
3	5	1	1	4	3	3	6	3	3	—	1	—	—	—	—	—	—	35	31.6
3	1	1	—	—	2	—	—	1	2	—	1	—	—	—	—	—	—	28	25.9
—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	50	21.6
11	18	17	35	34	37	28	14	7	1	—	—	—	—	—	—	—	—	206	30.9
—	—	1	—	—	—	—	1	1	—	1	—	—	—	—	—	—	—	4	33.8
5	3	—	6	5	7	8	16	25	12	12	5	1	—	—	—	—	—	107	33.8
6	8	9	9	6	8	12	24	17	21	14	5	3	1	—	—	—	—	153	32.9
3	6	5	5	4	5	6	3	8	3	4	1	2	1	—	—	—	—	71	30.5
14	16	10	11	8	4	3	—	4	—	—	—	—	—	—	—	—	—	102	27.3
10	16	16	13	5	4	—	—	—	—	—	—	—	—	—	—	—	—	91	27.3
—	—	—	—	—	3	2	—	3	1	5	5	5	3	8	6	—	—	42	38.1
1	2	2	1	4	9	10	7	6	1	1	1	—	—	—	—	—	—	47	32.6
—	—	—	—	1	1	1	3	9	7	14	6	5	6	1	1	—	—	55	36.9
—	—	1	5	5	8	12	10	4	2	1	1	—	2	—	—	—	—	51	33.2
—	—	—	—	—	—	2	1	1	3	—	—	1	—	—	—	—	—	8	35.3
—	—	—	—	—	—	—	3	11	19	41	45	31	27	15	5	4	—	201	38.2
10	9	12	4	—	2	1	—	3	—	—	—	—	—	—	—	—	—	59	27.9
—	1	2	2	11	5	2	4	1	—	—	—	—	—	—	—	—	—	28	31.6
5	1	8	11	10	4	3	6	4	3	—	1	—	—	—	—	—	—	62	30.8

Total: 1.801 specimens

Table 13. Whitefish samples from various

Lake, locality	Date	Size	16	17	18	19	20	21	22	23	24	25
Norrström River												
Hjälmaren	Nov. 50	—	—	—	—	—	—	—	—	—	—	—
S. Hörken	Oct. 55	—	—	—	—	—	—	—	—	—	—	—
Mälaren	Nov. 50—Jan. 55	—	—	—	—	—	—	—	—	—	—	—
Motalaström River												
Nätaren	Nov. 51	—	—	—	—	—	—	—	—	—	—	—
Ylen	Nov. 51	—	—	—	—	—	—	—	—	—	—	1
Vättern	Oct. 50—Dec. 54	—	—	—	—	—	3	5	19	31	37	46
» (Aspa)	Nov. 51	*389	—	—	—	—	—	1	1	5	8	7
» (Motala)	Jan. 51	*339	—	—	—	—	1	2	4	9	10	9
Unden	Dec. 50—53	< 350	—	—	—	—	—	—	—	—	—	—
»	Dec. 55—Jan. 56	> 350	—	—	—	2	1	2	4	5	5	7
Kyrksjön	Nov. 51	—	—	—	—	—	—	—	—	—	—	—
Narven	Nov. 49—Dec. 50	< 410	—	—	—	—	—	—	—	—	—	—
»	Nov. 49—Dec. 50	> 410	—	—	—	1	1	—	—	—	—	—
Ören	Apr. 57	—	—	1	—	1	5	2	2	4	—	—
Sommen	Dec. 55	—	1	—	3	9	24	27	28	15	5	1
Mossjön	Nov. 50	—	—	—	—	—	—	—	—	—	—	—
Åländern	Dec. 53	—	—	—	—	—	—	—	—	—	—	—
Drögen	Nov. 49—Dec. 54	< 400	—	—	—	—	—	—	1	—	—	1
»	Nov. 49—Dec. 54	> 400	—	—	1	2	4	4	5	2	2	1
Emån River												
Assjön	Nov. 51—54	—	—	—	—	—	—	—	—	—	—	1
Vallsjön	Nov. 51	—	—	—	—	—	—	—	1	1	3	7
Fagerhultssjön	Oct. 51	—	—	—	—	—	—	—	—	—	—	—
Alsterån River												
Alstern	Dec. 51	—	—	—	—	—	—	—	—	—	—	—
Mie River												
Mien	Nov. 51	—	—	—	—	—	—	—	—	—	—	1
Mörrumsån River												
Åsnen	Nov. 51	—	—	—	—	—	—	—	—	—	—	—
Skräbeån River												
Immeln	Dec. 51	—	—	—	—	—	—	—	—	—	—	—

* Mean size of the sample; all fish spawners.

small rivers in southeastern Sweden.

26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	Sample	Mean
—	—	—	—	—	—	—	—	—	—	—	—	1	9	8	5	4	1	2	1	—	31	40.6
—	—	1	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	30.0
—	—	4	7	15	9	9	10	6	—	—	—	—	—	—	—	—	—	—	—	—	60	31.1
—	—	—	—	1	—	1	1	—	—	2	2	1	4	4	3	—	—	1	—	—	20	38.1
—	1	—	1	2	1	4	4	3	1	1	5	3	2	—	—	—	2	—	—	—	31	34.5
24	16	15	5	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	203	24.7
10	5	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	40	25.1
12	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	48	24.2
—	—	1	4	12	14	23	25	10	7	3	2	—	—	—	—	—	—	—	—	—	101	32.3
7	8	3	3	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	49	25.1
—	—	—	—	—	—	1	3	3	5	5	7	6	—	—	—	—	—	—	—	—	30	35.8
1	2	5	1	6	4	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	22	29.6
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	19.5
—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	(20.9)
—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	114	(21.2)
—	—	—	—	—	—	—	—	—	1	—	—	2	2	3	2	3	—	—	—	—	13	39.8
—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	3	3	4	6	4	1	24	42.9
13	14	18	21	24	28	18	4	2	—	—	—	—	—	—	—	—	—	—	—	—	144	29.4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	21	21.4
4	4	17	21	16	12	16	8	1	1	—	—	—	—	—	—	—	—	—	—	—	101	29.9
8	4	1	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	27	25.9
—	—	—	—	—	2	5	6	5	3	4	1	1	2	—	1	—	—	—	—	—	30	34.4
—	—	—	—	—	—	—	—	1	—	1	7	8	10	9	8	4	2	—	—	—	50	39.3
3	5	9	8	12	9	2	1	2	—	—	—	—	—	—	—	—	—	—	—	—	52	29.3
—	—	—	—	—	—	1	4	5	9	20	10	6	2	1	—	—	—	—	—	—	58	35.9
—	—	—	—	1	—	1	4	4	8	5	8	3	1	—	—	—	—	—	—	—	35	35.4

Total: 1.325 specimens

Table 14. Whitefish samples from various

Lake, locality	Date	Size	16	17	18	19	20	21	22	23	24	25
Rönne River												
Ringsjön[1]	1872—1882	—	—	—	—	—	—	—	—	—	—	—
»	Nov. 52	—	—	—	—	—	—	—	—	—	—	—
Lagan River												
Övringen	Dec. 51—54	—	—	—	—	—	—	—	—	—	—	—
Allgunnen	Nov. 44—55	—	—	—	—	—	—	—	—	—	—	—
»	Nov. 55	—	—	—	—	—	—	—	—	—	—	2
Rusken	Nov. 51	—	—	—	—	—	—	—	—	—	—	—
Flåren[1]	Oct. 77	—	—	—	—	—	—	—	—	—	—	—
»	Nov. 51	—	—	—	—	—	—	—	—	—	—	—
Hindsen[1]	Jan. 77	—	—	—	—	—	—	—	2	—	—	—
»	Nov. 54	—	—	—	—	—	—	3	4	8	6	1
Vidöstern[1]	Oct. 77	—	—	—	—	—	—	—	—	—	—	—
Bolmen[1]	Nov. 70	—	—	—	—	—	—	—	—	—	—	—
»	Nov. 51—54	—	—	—	—	—	—	—	—	—	—	—
Nissan River												
Stengårdshultsjön	Nov. 51	—	—	—	—	—	—	—	—	—	—	2
Ätran River												
Åsunden	Mar. 56	—	—	—	—	—	—	—	1	—	1	—
Såken	Nov. 51	—	—	—	—	—	—	—	—	—	1	—
Sämsjön[2]	Nov. 29	—	—	—	1	—	3	5	1	1	—	—
»	Nov. 51—55	—	—	—	2	6	15	7	9	7	2	—
Visen	Nov. 51—Dec. 54	—	—	—	—	—	—	—	—	—	—	—
Fegen	Nov. 55	—	—	2	5	11	10	12	3	1	—	—
Yttre Hallången	Nov. 51—54	—	—	—	—	—	—	—	—	—	—	2
Viskan River												
Tolken (Ås)[2]	Aug. 33	—	—	—	—	—	—	—	—	—	—	—
»	Nov. 51	—	—	—	—	—	—	—	—	—	—	—
Ärtingen[2]	Nov. 25	—	—	—	—	—	—	1	1	1	—	1
Öresjön[2]	Nov. 25	—	—	—	—	—	1	1	1	1	3	—
»	Nov. 55	—	—	—	—	—	—	1	—	—	2	—
St. Holsjön	May 56	—	—	1	1	2	1	—	—	—	—	—
Tolken (Mark)[2]	Nov. 20	—	—	—	—	—	—	—	—	—	—	—
»	Nov. 51	—	—	—	—	—	—	—	—	—	—	2
Kyrkälven River												
Södra Kornsjön	Jan. 52—Nov. 56	—	—	—	—	—	—	—	—	—	—	—
Bullaren[1]	Dec. 73	—	—	—	—	—	—	—	—	—	—	—
»	Dec. 54	—	—	—	—	—	—	—	—	—	—	—
Randselva River												
Randsfjorden[3]												
»Strømsik»		—	—	—	—	—	—	—	—	—	—	—
»Grunnsik»		—	—	—	—	—	—	—	—	—	1	1
»Vintersik» »Djupvannsik»		—	—	—	—	—	—	—	—	—	—	1

[1] Material in the museums of Gothenburg and Stockholm.
[2] From unpublished notes by the late Dr. T. Freidenfelt.
[3] From Enge (unpublished).

small rivers in southwestern Scandinavia.

26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	Sample	Mean
—	—	—	—	—	—	—	1	1	5	9	6	10	4	3	—	1	—	—	—	—	40	37.2
—	—	—	—	—	—	—	—	1	3	5	6	8	2	3	1	1	—	—	—	—	30	37.5
—	—	—	1	2	—	—	1	3	4	8	13	9	4	9	—	1	—	—	—	—	55	37.0
1	—	—	2	—	1	1	3	2	9	8	18	19	10	4	1	—	—	—	—	—	79	36.7
3	2	5	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15	27.5
—	—	—	—	—	—	—	1	—	—	3	3	4	6	3	4	2	1	1	—	—	28	39.0
—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	3	38.0
—	—	—	—	—	—	—	—	—	—	5	4	2	4	4	3	—	—	—	—	—	22	38.3
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	22.0
1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	25	23.4
—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	—	—	—	—	—	—	3	39.7
—	—	—	1	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	3	32.3
—	—	—	—	2	2	3	9	7	2	5	2	1	1	—	—	—	—	—	—	—	34	33.9
5	4	8	5	3	2	2	—	—	—	—	1	—	—	—	—	—	—	—	—	—	32	28.4
—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	24.3
1	—	1	2	3	3	4	3	4	3	3	1	1	—	—	—	—	—	—	—	—	30	32.3
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12	21.2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	48	20.9
—	—	—	—	—	—	1	1	4	9	12	22	23	23	18	5	2	3	—	1	—	124	38.0
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	44	19.9
12	12	14	27	21	14	13	12	1	2	—	—	—	—	—	—	—	—	—	—	—	130	29.5
—	—	—	—	—	1	—	2	3	—	2	1	1	—	—	—	—	—	—	—	—	10	34.6
—	—	1	—	—	1	3	5	6	3	3	2	1	2	—	—	—	—	—	—	—	27	34.3
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	22.8
—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	23.3
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	23.0
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	18.6
1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	26.5
3	4	4	7	7	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	29	28.4
—	—	—	1	8	13	23	27	38	31	21	9	9	1	—	—	—	—	—	—	—	181	34.0
—	—	—	1	1	—	3	1	1	3	—	1	—	—	—	—	—	—	—	—	—	11	33.1
—	1	3	4	4	17	23	16	18	20	5	2	2	—	—	—	—	—	—	—	—	115	32.9
—	—	—	—	2	1	5	5	7	12	11	5	5	5	4	1	—	—	—	—	—	63	35.6
3	9	10	12	8	12	4	8	—	1	2	1	—	—	—	—	—	—	—	—	—	72	29.8
3	10	26	25	22	21	13	4	3	—	—	—	—	—	—	—	—	—	—	—	—	128	29.6

Total: 1.420 specimens

Table 15. Whitefish samples from

Lake, locality	Date	Size	19	20	21	22	23	24	25	26	27
Femunden	Oct.—Dec. 54	< 300	—	—	—	—	—	—	—	—	—
»	Oct.—Dec. 54	301—400	—	—	—	—	—	3	3	13	20
»	Oct.—Dec. 54	401—450	—	—	—	—	—	1	1	—	—
»	Oct.—Dec. 54	> 450	—	—	—	—	—	—	—	—	—
Tisjön	Sep.—Oct. 56	—	—	—	3	4	3	1	3	8	3
Kårebosjön	Jan. 55	—	—	—	—	—	—	—	—	—	—
Kasjön[1]	Dec. 30	—	—	—	—	—	—	—	—	—	—
Kvien[1]	Aug. 31	—	—	—	—	—	—	—	—	—	—
Tyngsjön[1]	Dec. 32	—	—	—	—	—	—	—	—	—	—
Nain[1]	Aug. 31	—	—	—	—	—	—	—	—	—	—
Bredsjön[1]	Dec. 32	—	—	—	—	—	—	—	—	—	—
St. Laggen[1]	Nov. 29	—	—	—	—	—	—	—	—	—	—
Mussjön[1]	Jul. 30	—	—	—	—	—	—	—	—	—	—
Knon[1]	Jul. 30	—	—	—	—	—	—	—	—	—	—
St. Ullen	Nov. 56	—	—	—	—	1	—	—	1	—	1
Ämten[1]	Dec. 30	—	—	—	—	—	—	—	—	—	1
»	Jan. 55	—	—	—	—	—	—	—	—	—	4
Ögsjön[1]	Sep. 30	—	—	—	—	—	—	—	—	—	—
Gröcken	May 56	—	—	—	—	—	—	—	1	—	—
Stor-Jangen[1]	1928—1932	—	—	—	—	—	—	—	—	—	—
»	Jan. 50—52	—	—	—	—	—	—	—	—	—	—
Fryken[1]	Dec. 22	—	—	—	—	—	—	—	—	—	—
»	Jun.—Dec. 56	—	—	—	—	—	—	—	—	—	—
Värmeln[1]	Nov. 25	—	—	—	—	—	—	—	2	—	1
»	Dec. 55	—	—	—	—	1	3	1	3	—	—
Hemsjön[1]	Nov. 29	—	—	—	—	—	—	—	—	—	2
»	Jan. 55	—	—	—	—	—	—	—	—	—	5
Övre Gla	Dec. 51	—	—	—	—	—	—	—	1	1	3
Stora Gla[1]	Nov. 15	—	—	—	—	—	—	—	—	—	—
» »	Nov. 49	—	—	—	—	—	—	—	—	—	—
Glafsfjorden[1]	Nov. 24	—	—	—	—	—	—	—	—	—	—
Öjesjön	Nov. 56	—	—	—	—	—	—	—	—	—	—
Lelången	Nov. 49—51	—	—	—	—	—	—	—	—	—	—
Yngen	Jan. 56	—	2	1	9	16	26	17	17	18	12
Skagern[1]	1922—1923	—	—	—	—	—	—	—	—	—	—
»	Nov. 51—Jan. 57	—	—	—	—	—	—	—	—	—	—
Jogen[1]	Nov. 23	—	—	—	—	—	—	—	—	—	1
Vänern											
Hammarö[1]	1923	—	—	—	—	—	—	2	4	2	—
»	Nov. 52—Dec. 54	—	—	—	—	—	—	—	1	—	1
Åråsviken[1]	1917	—	—	—	2	5	3	4	3	1	1
»	Nov. 51	—	—	—	1	3	5	4	9	3	4
Vänersnäs[1]	1918—1924	—	—	2	1	2	10	10	18	16	9
»[1]	1912—1924	—	—	—	—	1	—	1	3	5	2
Mellerud	Dec. 53	—	—	—	—	—	—	1	—	1	3
Kinneviken[1]	Oct. 22	—	—	—	—	—	—	4	3	5	8
»	Nov. 50—Jan. 54	—	—	1	1	1	8	3	9	11	12
Kållandsö	Oct. 50—Nov. 51	—	—	—	1	1	3	12	6	7	8
»	Oct.—Nov. 51	—	—	—	—	—	—	—	—	1	3
Göta River											
Lilla Edet	Nov. 52	—	—	1	1	2	—	4	6	2	2
Archipelago off[2] the river's mouth	1850—1920	—	—	—	1	1	4	6	4	2	1

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[1] From unpublished notes by the late dr. T. FREIDENFELT.

[2] Material in the museum of Gothenburg.

the Klarälven-Götaälv river system.

28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	Sample	Mean
—	—	—	—	—	1	—	1	—	1	1	—	—	3	2	2	2	2	—	—	—	—	—	—	13	40.9
23	14	21	15	3	8	5	10	17	5	9	—	—	—	—	1	—	2	2	—	1	1	—	—	176	31.3
3	7	3	6	6	27	26	41	35	40	19	5	3	1	3	4	9	4	6	7	3	—	—	1	261	36.4
—	3	—	1	2	3	3	1	4	2	2	1	5	1	4	15	10	12	10	7	4	3	—	—	93	42.1
4	6	3	3	5	4	4	10	2	—	3	4	1	1	1	—	—	—	—	—	—	—	—	—	76	30.5
—	—	—	4	4	4	5	4	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23	33.3
—	3	1	3	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	30.4
—	—	1	2	5	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	32.1
—	—	—	—	2	2	3	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	33.7
—	1	1	—	1	2	2	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	32.9
—	—	—	3	1	—	4	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	33.5
—	—	—	—	1	1	2	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	34.1
2	1	2	2	—	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	30.7
—	—	—	—	—	—	—	1	3	2	—	2	1	—	—	—	—	—	—	—	—	—	—	—	9	37.2
—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	27.2
1	1	6	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	29.6
4	12	10	4	4	1	—	1	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	41	(29.7)
—	—	—	—	—	—	2	4	3	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	35.5
—	—	—	—	—	1	—	1	2	1	—	1	2	—	—	—	—	—	—	—	—	—	—	—	9	35.7
—	—	—	—	—	—	—	—	1	1	3	—	—	—	—	—	—	—	—	—	—	—	—	—	5	37.4
—	—	—	1	—	—	—	1	3	6	3	3	5	2	1	—	—	—	—	—	—	—	—	—	25	38.0
—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	3	3	1	2	—	—	1	—	—	12	44.2
—	—	—	—	—	—	—	1	1	—	—	2	2	1	8	5	2	3	4	2	1	—	1	—	33	43.0
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	25.7
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	23.8
2	2	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	29.0
8	16	15	11	2	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	60	29.7
7	3	3	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	20	28.8
—	—	—	—	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	33.0
—	—	—	—	—	—	—	5	2	4	5	10	7	7	1	4	1	1	—	1	—	—	—	—	48	39.4
—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	30.5
—	—	—	—	—	—	—	—	2	5	5	6	11	5	4	2	—	—	—	—	—	—	—	—	40	39.5
—	—	—	—	—	1	2	3	3	9	7	5	2	1	2	—	—	—	—	—	—	—	—	—	35	37.5
9	1	1	3	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	135	24.6
—	—	—	—	1	1	5	—	2	3	4	—	—	1	—	—	—	—	—	—	—	—	—	—	17	35.9
—	—	—	1	1	5	7	13	20	12	12	13	10	3	1	—	—	—	—	—	—	—	—	—	98	36.9
2	2	3	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	29.6
—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	25.9
3	4	8	8	14	14	19	12	13	6	5	4	1	—	—	—	—	—	—	—	—	—	—	—	113	33.6
—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	23.7
1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	31	24.7
5	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	79	25.3
8	16	15	6	10	6	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	74	29.5
3	6	2	1	1	—	3	—	1	1	—	—	—	—	1	—	—	2	—	—	—	—	—	—	26	31.5
4	5	1	1	4	1	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	40	28.1
7	8	11	10	8	12	7	7	5	5	2	3	2	—	—	—	—	—	—	—	—	—	—	—	133	30.0
2	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	43	25.4
3	7	11	7	11	8	5	6	4	1	2	—	1	—	—	1	1	—	—	1	1	—	—	—	74	32.6
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	18	24.3
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	19	24.1

Total: 2.035 specimens

Table 16. Whitefish

Rivers discharging into the Baltic Sea or

		23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
River Kemi																	
Saukkojärvi	1932	—	—	—	—	—	—	—	—	1	1	7	7	7	6	1	2
Pikku-Kaarnijärvi	1928	—	—	—	—	—	—	—	—	1	7	5	10	18	14	24	13
»	1929	—	—	—	—	—	—	—	—	—	—	5	10	10	9	10	12
»	1930	—	—	—	—	—	—	—	—	—	1	3	8	14	8	14	7
»	1931	—	—	—	—	—	—	—	—	1	1	5	5	7	7	7	4
»	1943	—	—	—	—	—	—	—	—	—	—	1	5	7	6	4	1
Marasenjärvi	1943	—	—	—	—	—	—	—	—	—	—	1	7	11	15	19	9
Latvajärvi	1943	—	—	—	—	—	—	—	—	—	—	—	—	6	—	3	6
Karhujärvi	1943	—	—	—	—	—	—	—	—	—	—	—	1	1	2	3	7
Kivalikkolampi	1931	—	—	—	—	—	—	—	—	—	—	—	1	2	2	—	1
Sonkajärvi	1915	—	—	—	—	—	—	2	1	5	16	12	10	10	4	—	2
Sinättäjärvi	1924	—	—	—	—	—	—	—	4	4	11	26	25	18	7	—	5
Paatinkii	—	—	—	1	2	8	7	9	7	7	—	1	—	—	—	—	—
River Simojoki																	
Simojärvi		—	2	—	6	7	4	14	11	10	8	—	—	—	—	—	—
River Iijoki																	
Kero		2	5	13	15	15	17	21	8	13	3	3	3	—	—	—	—
Kavajärvi		—	—	1	1	—	—	3	4	7	9	13	17	20	21	14	11
River Kumo																	
Jamajärvi	1929	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Murole	1925	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Kyrösjärvi	1940	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Kaartjärvi	1925	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
River Kymmene																	
Päijänne	1938	—	—	—	—	—	—	—	—	6	2	2	10	10	9	2	5
»	1939	—	—	—	—	—	—	1	1	2	3	6	9	15	7	1	2
»	1940	—	—	—	—	—	—	—	—	—	4	4	5	5	11	13	10
Peruvesi	1927	—	—	—	—	—	—	—	—	—	—	—	—	2	1	3	8
Leppävesi	1925	—	—	—	—	—	—	—	—	—	4	5	3	7	8	5	—
Keitele	1924	—	—	—	—	—	—	—	—	—	1	3	1	8	8	12	24
Lievestuore		—	—	—	—	—	—	—	—	—	2	4	3	5	—	3	1
Saima-Vuoksen																	
Kivijärvi		—	—	—	—	—	—	—	—	—	—	—	1	3	4	7	4
Koitere		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

populations in Finland.

Lake Ladoga (rearranged from JÄRVI 1928—1953).

39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	Sample	Mean
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	32	34.6
2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	96	35.8
4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	60	36.0
3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	58	35.9
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	38	35.4
1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	26	35.7
6	5	4	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	79	37.0
3	3	4	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	28	38.5
5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	37.7
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	35.7
1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	64	33.4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	100	33.8
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	42	28.8
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	62	29.1
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	118	28.0
5	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	130	34.7
—	—	—	—	1	1	—	2	—	—	2	1	—	1	2	—	—	—	—	—	10	48.5
—	—	—	—	5	2	5	13	21	10	24	13	11	9	4	4	2	1	—	—	124	48.7
—	—	—	—	—	—	—	2	—	3	1	4	—	—	2	—	—	—	—	—	12	49.2
—	13	23	27	28	16	8	5	—	—	—	—	—	—	—	—	—	—	—	—	120	42.4
2	2	—	—	2	2	1	1	—	—	—	—	1	3	—	1	—	1	—	—	62	37.6
4	3	—	1	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	58	35.5
6	2	2	2	1	1	—	—	1	1	—	1	—	–	1	—	—	—	—	—	70	37.5
9	7	4	3	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	40	39.3
3	2	3	6	5	2	7	15	8	4	1	—	6	—	—	—	—	—	—	—	94	41.7
26	16	12	10	3	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	126	38.7
2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	35.0
2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	22	36.9
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	2	2	6	56.7

Table 17. Whitefish

Rivers discharging into the White Sea and the Arctic

	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
River Paatsjoki																
Vuontisjärvi	—	—	—	1	1	—	—	—	—	—	1	5	9	14	16	15
Inari, Palttenemi	—	—	—	—	1	11	20	18	42	37	30	17	12	5	3	3
Muddusjärvi	—	—	—	—	—	1	7	2	4	8	10	4	—	—	—	—
Inari, Juutuanjoki	—	—	—	—	—	1	2	4	3	2	4	2	—	—	—	—
Inari, Virtaniemi	—	—	—	—	—	—	2	5	5	2	—	—	—	—	—	1
Tiaisjärvi	—	—	—	—	—	—	—	3	1	8	5	6	1	2	—	—
Tshuolisjärvi	—	—	—	—	—	—	—	—	—	—	—	1	2	1	1	1
River Kovda																
Yli-Kitka	—	—	1	4	4	5	7	8	8	8	19	11	17	4	1	3
Kallunki	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
»	1	—	4	1	—	1	1	—	—	—	—	—	—	—	—	—
Kiitämä	—	2	1	4	13	11	12	6	1	3	1	1	1	1	—	—
Suinunki	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—
Porontimo	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sulkajärvi	—	—	—	—	1	1	4	3	1	—	—	—	—	—	—	—
Kulmakka	—	—	—	—	—	—	—	1	1	1	1	—	—	—	—	—
Laihajärvi	—	—	—	—	—	2	8	19	14	13	8	—	2	—	—	—
Vatajärvi	—	—	—	—	4	4	11	15	13	11	10	9	1	—	—	—
Tavajärvi	—	—	—	—	3	12	21	11	8	8	7	—	—	—	—	—
Koupsijärvi	—	—	—	1	5	13	15	24	16	5	1	—	—	—	—	—
River Kem																
Salmijärvi	—	—	—	1	4	9	11	6	11	13	4	1	—	—	—	—
Kuusamojärvi	—	—	1	4	6	11	8	7	1	2	—	—	—	—	—	—
Toranki	—	—	—	—	—	6	4	13	10	5	7	2	2	1	—	—
Kirpistö	—	—	—	—	—	—	—	—	1	4	1	7	11	10	3	5
Kopatti	—	—	—	2	8	7	3	—	—	—	—	—	—	—	—	—

populations in Finland.

Ocean (rearranged from JÄRVI 1928—1953).

30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	Sample	Mean
28	5	3	—	2	—	—	—	—	—	—	—	—	—	—	—	100	28.4
4	5	7	11	5	5	4	—	—	—	—	—	—	—	—	—	240	24.6
—	1	1	1	1	—	2	—	—	—	—	—	—	—	—	—	42	24.2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	18	22.3
3	3	12	3	12	1	5	—	—	—	—	—	—	—	—	—	54	30.0
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	26	23.8
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	26.8
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	100	23.2
—	2	2	9	6	5	1	1	—	—	—	—	—	—	—	—	26	33.7
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	16.7
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	57	19.6
4	5	4	10	17	11	10	4	2	7	—	—	—	—	—	—	76	34.2
—	—	—	1	1	—	2	7	3	—	2	1	1	—	—	—	18	37.5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	20.2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	22.5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	66	21.9
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	78	22.0
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	70	20.9
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	80	20.6
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	60	21.1
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	40	19.4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	50	22.0
9	5	4	—	—	—	—	—	—	—	—	—	—	—	—	—	60	27.5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	18.6

Table 18. Whitefish populations of the Carelian and adjacent

Locality	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
The Gulf of Finland..	—	—	—	—	—	—	2	2	3	1	1	3	1	—	1	—	—	—	—	—
Peipus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	3
Neva	—	—	—	—	—	1	5	13	8	13	—	3	2	—	—	—	—	1	—	—
Ladoga	—	—	—	4	4	5	9	11	15	12	5	1	—	1	—	—	—	—	—	—
Volchov	—	—	—	1	5	16	26	32	31	9	2	2	2	—	—	—	—	—	—	—
Swirs' mouth	—	—	—	—	1	3	11	24	21	10	4	3	2	2	2	—	—	—	—	—
Nimpelda	—	—	—	2	8	7	33	26	32	23	18	9	2	2	1	—	1	—	—	—
Voznesene	—	—	—	—	5	7	2	8	5	4	—	—	—	—	—	—	—	—	—	—
Onega	—	—	—	—	—	1	2	4	2	7	8	14	20	19	6	4	1	2	1	—
Vodla	—	—	—	—	—	—	—	—	—	2	8	11	17	45	41	25	12	22	5	3
Suna	—	—	—	—	—	—	—	—	—	—	1	4	7	8	24	42	51	65	44	22
Logm	—	—	—	—	—	—	—	—	—	—	1	—	2	1	2	3	2	2	—	1
Uksch	—	—	—	—	—	—	—	—	—	1	1	—	1	—	3	6	4	3	3	3
Surgub	—	—	—	—	—	—	—	—	—	—	—	1	1	1	—	1	1	3	1	1
Pert	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Padm	—	—	—	—	—	—	—	—	—	1	1	—	2	3	3	2	3	—	—	—
Sund	—	—	—	—	—	—	—	—	1	—	2	3	3	1	—	—	—	—	—	—
Pjal	—	1	2	7	4	2	5	2	1	—	—	—	—	—	—	—	—	—	—	—
Sjam	2	—	1	1	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Vocht	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Kuito	—	—	—	—	—	—	—	—	—	—	—	—	1	2	7	9	17	12	10	5

regions of the U.S.S.R. (rearranged from PRAVDIN 1931).

37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	Sample	Mean
—	—	13	1	3	2	6	—	—	2	1	—	—	—	—	—	—	—	—	—	42	36.1
11	16	4	9	9	3	3	1	1	—	—	—	—	—	—	—	—	—	—	—	62	39.1
1	—	2	2	8	13	4	3	6	2	3	4	—	—	—	—	—	—	—	—	94	34.4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	67	24.2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	126	24.0
—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	84	25.2
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	165	24.8
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	31	23.4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	91	28.6
3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	194	31.1
20	9	5	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	304	33.7
2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	32.3
2	2	—	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	31	34.0
—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12	33.5
9	1	6	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	37.8
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15	30.5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	28.0
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	24	21.3
—	—	—	—	1	1	—	—	1	1	—	2	1	3	1	—	—	—	—	1	18	38.5
—	—	—	—	1	—	1	—	—	2	—	—	—	—	—	—	—	—	—	—	4	44.0
3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	66	33.4

Table 19. Whitefish populations in Denmark (rearranged from OTTERSTRØM 1922).

Locality	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	Sample	Mean
Nipså	—	—	—	—	—	1	2	—	—	2	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	6	33.3
Ringkjöbing Fjord	—	—	—	1	—	1	1	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	31.4
Nissum Fjord	—	1	—	—	3	1	3	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	30.1
Fladesö	—	—	—	—	—	—	—	—	1	4	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	7	35.1
Ovesö	—	—	—	—	—	—	—	—	—	1	1	—	2	1	—	—	—	—	—	—	—	—	—	—	—	5	36.2
Flyndersö	—	—	—	—	—	—	—	—	1	—	—	1	2	—	—	—	—	—	—	—	—	—	—	—	—	4	35.8
Stubbergård Sö	—	—	—	—	—	—	—	—	—	—	1	1	—	—	1	1	—	—	—	—	—	—	—	—	—	4	37.5
Kragsö	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	34.0
Hjarbaek Fjord	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	1	1	—	—	4	41.0
Klejtrup Sö	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	2	—	1	1	—	—	—	5	43.2
Glenstrup Sö	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	1	2	4	—	10	46.4
Tjele Langsö	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1	2	—	7	1	—	—	—	13	43.7
Randers Fjord	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	30.0

Table 20. Whitefish populations in the British Isles (through the courtesy of Dr. E. DOTTRENS).

Lake	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	47	Sample	Mean
Lough Erne	—	—	—	—	—	—	—	—	—	1	1	—	6	21	18	23	14	13	5	1	1	—	104	41.8
Lough Neagh	—	—	—	—	—	—	—	—	2	11	20	28	17	15	4	1	—	—	—	—	—	—	98	38.2
Loch Lomond (British Museum)	—	—	—	1	2	6	2	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	14	32.4
» »	—	1	1	9	19	44	70	100	78	39	12	5	1	—	—	—	—	—	—	—	—	—	379	33.9
Ullswater (British Museum)	—	—	—	—	—	—	—	—	—	—	—	1	—	—	3	—	—	—	—	—	—	—	4	40.2
» »	—	—	—	—	—	—	—	3	7	13	13	10	10	2	—	1	—	—	—	—	—	—	59	37.1
Haweswater (British Museum)	—	—	—	—	—	—	—	—	1	—	2	1	2	—	—	—	—	—	—	—	—	—	6	37.5
» »	—	—	—	—	—	—	—	1	2	7	8	4	6	4	2	—	—	—	—	—	—	—	34	37.6
Lake Bala (Brit. Mus.; Univ. Liverpool)	—	—	—	—	1	1	1	—	2	2	4	7	8	4	—	—	—	—	—	—	—	—	30	37.5

Table 21. Whitefish populations of the Alpine

Lake	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Constance	1	1	8	8	18	27	21	17	3	1	—	—	—	—	—
»	—	—	—	1	3	12	26	33	43	29	15	8	9	3	2
»	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
»	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Thuner See	—	1	1	5	4	10	20	12	4	3	—	—	—	—	—
»	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
»	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sempacher See	—	—	—	—	—	—	—	—	—	2	—	3	5	3	2
»	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Zürichsee	—	—	—	—	—	—	—	—	1	1	1	1	1	2	1
»	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ammersee	—	—	—	—	2	—	3	16	12	8	4	3	—	2	—
»	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Attersee	—	—	—	—	—	—	—	—	—	1	2	1	6	1	3
»	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chiemsee	—	—	—	—	—	2	4	8	19	15	17	24	11	9	3
»	—	—	—	—	—	—	—	—	2	—	3	15	15	16	14
Wallensee	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
»	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Vierwaldstätter See	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
»	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Greifensee	—	—	—	—	—	—	—	—	1	—	3	—	2	7	5
Alpsee	—	—	—	—	—	—	—	—	1	—	2	2	6	19	23
Pfäffikonsee	—	—	—	—	—	—	—	—	1	1	1	4	6	9	7
Mondsee	—	—	—	—	—	—	—	—	—	—	—	—	2	5	15
Weissensee	—	—	—	—	—	—	—	—	—	—	—	—	2	1	3
Kochelsee	—	—	—	—	—	—	—	—	—	—	—	1	1	2	—
Bieler See	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Walchensee	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Baldegger See	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tegernsee	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Hallwiler See	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Plansee	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Achensee	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Würmsee	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Wörther See	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Abersee	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Faaker See	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Wörthsee	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Staffelsee	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hallstätter See	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

region (rearranged from WAGLER, 1937).

30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	Sample	Mean
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	105	20.0
2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	189	23.2
—	—	—	10	17	26	30	27	22	15	4	2	2	—	—	—	—	—	155	36.4
—	—	—	1	2	4	4	13	12	16	21	30	19	22	8	2	2	1	157	40.4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	60	20.8
—	—	—	—	—	1	5	5	2	3	2	—	—	—	—	—	—	—	18	37.4
—	—	—	—	—	—	1	—	3	4	3	10	18	11	3	4	2	—	59	41.8
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15	26.9
2	2	7	7	7	5	9	4	—	2	—	—	—	—	—	—	—	—	46	34.1
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	26.7
—	—	—	—	5	8	4	2	—	—	—	—	—	—	—	—	—	—	19	35.2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	50	23.1
—	4	4	8	13	21	17	15	10	4	1	—	—	—	—	—	—	—	97	35.2
2	3	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	21	28.4
1	2	2	18	15	19	9	13	3	1	—	—	—	—	—	—	—	—	83	34.7
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	113	24.9
17	7	3	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	94	28.3
1	2	1	6	8	20	17	16	9	8	1	—	—	—	—	—	—	—	91	35.7
—	1	1	4	9	25	18	21	16	11	5	—	—	—	—	—	—	—	111	36.2
—	—	—	2	7	10	8	20	17	10	7	5	4	—	—	—	—	—	90	37.5
—	—	—	—	1	3	7	8	18	21	28	16	11	7	—	—	—	—	120	39.4
6	2	3	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	32	29.1
11	19	7	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	92	29.4
14	11	6	2	1	2	1	2	—	—	—	—	—	—	—	—	—	—	68	29.8
19	28	20	10	5	2	1	—	—	—	—	—	—	—	—	—	—	—	107	31.0
4	12	4	9	8	10	5	1	—	—	—	—	—	—	—	—	—	—	59	32.6
4	12	22	17	13	10	4	2	—	—	—	—	—	—	—	—	—	—	88	32.7
2	1	6	3	8	5	4	3	1	—	—	—	—	—	—	—	—	—	35	33.7
—	3	2	2	8	2	5	—	—	—	—	—	—	—	—	—	—	—	22	33.9
—	6	11	15	25	13	12	3	3	1	—	—	—	—	—	—	—	—	89	34.1
—	2	4	12	21	27	13	15	2	3	—	—	—	—	—	—	—	—	100	34.9
—	—	—	2	7	3	6	5	2	—	—	—	—	—	—	—	—	—	25	35.4
—	—	—	—	1	8	16	25	21	12	10	2	1	—	—	—	—	—	96	37.6
—	—	—	—	2	8	18	29	22	17	8	4	2	1	—	—	—	—	111	37.6
—	—	—	1	3	10	10	16	21	17	10	2	4	1	—	—	—	—	95	37.8
—	—	—	—	—	—	1	2	1	—	3	1	1	—	—	—	—	—	9	39.0
—	—	—	—	1	1	2	15	12	18	24	18	6	2	1	—	—	—	100	39.3
—	—	—	—	—	—	1	2	14	20	22	24	13	2	1	2	—	—	101	40.1
—	—	—	—	1	2	4	3	9	19	17	18	10	10	3	2	2	—	100	40.2
—	—	—	—	—	—	1	4	9	5	10	18	21	13	7	6	3	1	98	41.5
—	—	—	—	—	—	—	1	1	6	13	31	28	22	13	13	1	3	132	42.2

Table 22. Cisco samples from Swedish localities.

Lake, locality	Date	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	Sample	Mean
Kalix archipelago	Nov. 54	—	—	—	—	—	—	3	5	16	11	12	15	5	2	2	—	—	—	—	71	46.6
» »	Nov. 55	—	—	—	2	4	4	14	15	15	14	10	1	5	—	—	—	—	—	—	84	44.7
» »	Oct. 56	—	1	—	7	11	14	21	20	11	14	7	3	—	—	—	—	—	—	—	109	43.6
Lule archipelago	Nov. 54	—	—	—	—	1	4	6	9	17	17	13	11	10	4	2	—	1	—	—	95	46.3
Gråträsket, River Byske	Sep. 56	5	36	12	40	19	20	9	1	—	—	—	—	—	—	—	—	—	—	—	142	39.9
Järvträsket, River Skellefte	Dec. 51	1	2	3	5	5	5	3	2	1	—	—	—	—	—	—	—	—	—	—	27	41.0
Sörsjön, River Ångermanälven	Aug. 56	—	3	6	12	15	11	19	18	7	6	3	—	—	—	—	—	—	—	—	100	42.5
Holmsjön, River Ljungan	Nov. 57	—	—	—	—	—	—	—	—	3	3	1	3	1	—	1	—	1	—	—	13	47.5
Siljan, River Dalälven	Nov. 54	—	—	1	2	8	17	14	19	15	15	6	4	—	—	—	—	—	—	—	101	43.9
Öjesjön » »	Nov. 54	—	—	—	—	2	2	4	6	11	5	8	2	—	—	—	—	—	—	—	40	45.0
Busjön » »	Nov. 51	—	—	—	1	3	4	4	5	12	7	3	4	2	—	—	—	—	—	—	45	44.8
Kvicksund, Lake Mälaren	Nov. 40	—	—	—	2	3	5	12	13	21	12	8	2	—	—	1	—	—	—	—	79	44.6
» » »	Nov. 41	—	—	3	5	11	10	18	23	10	9	7	3	—	—	—	—	—	—	—	99	43.5
Tidö, » »	Nov. 54	—	—	—	—	1	5	11	14	18	23	14	6	6	5	1	—	—	—	—	104	45.7
Lambarfjärden, Lake Mälaren	Oct. 55	—	—	1	—	2	5	10	16	16	13	12	9	1	2	1	—	—	—	—	88	45.2
Vättern	Sep. 51	—	—	—	—	—	—	—	—	5	8	9	11	8	2	4	—	—	—	1	48	47.8
»	Nov. 54	—	—	—	—	—	—	—	2	2	4	1	8	5	—	1	—	—	—	—	23	47.3
»	Dec. 55	—	—	—	—	—	1	2	1	6	2	1	1	1	—	—	—	—	—	—	15	45.2
»	Nov. 56	—	—	—	1	1	4	8	3	6	4	4	2	—	—	—	—	—	—	—	33	44.3
Ören (Gränna)	Nov. 56	—	—	1	6	7	20	25	23	17	11	7	—	—	—	—	—	—	—	—	117	43.3
» » (*baunti*)	Apr. 57	—	—	3	5	11	23	30	31	13	11	1	1	—	—	—	—	—	—	—	129	43.2
Sommen	Nov. 54	—	1	—	1	1	4	9	18	19	26	10	6	2	1	—	—	—	—	—	98	45.1
Skagern	Nov. 54	—	—	—	—	—	—	10	24	37	56	47	29	20	19	7	5	—	—	—	254	46.8
Hammarö, Lake Vänern	Nov. 55	—	2	2	4	6	14	16	24	13	6	5	4	1	—	—	—	—	—	—	97	43.6
Kinneviken, » »	Nov. 55	—	1	6	8	10	11	21	17	30	10	8	1	1	—	—	—	—	—	—	124	43.5
Ånimmen	Nov. 56	—	—	—	2	2	5	8	7	9	12	4	1	—	—	—	—	—	—	—	50	44.3
St. Holsjön (*baunti*)	May 39	—	1	4	9	7	5	14	6	2	1	1	—	—	—	—	—	—	—	—	50	42.0
» » (*baunti*)	Apr. 53	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—
» »	May 56	—	1	—	—	1	1	3	1	1	1	1	—	—	—	—	—	—	—	—	10	43.2
» »	Nov. 40	—	—	—	1	4	8	10	18	5	9	2	1	—	—	—	—	—	—	—	58	43.8
» »	Nov. 52	—	—	—	—	1	1	8	7	1	1	—	—	—	—	—	—	—	—	—	19	43.5
» »	Nov. 53	—	—	1	3	5	10	13	11	5	2	—	—	—	—	—	—	—	—	—	50	42.9
Åsunden (*baunti*)	May 56	—	—	—	—	—	1	1	—	—	1	—	—	—	—	—	—	—	—	—	3	—
»	May 56	—	—	—	1	4	4	6	12	1	1	—	1	—	—	—	—	—	—	—	30	43.2
Anten	Dec. 54	—	—	2	1	7	16	23	29	29	21	12	5	1	—	—	—	—	—	—	146	44.3
Mjörn	Dec. 55	1	2	3	5	11	13	13	19	12	13	7	2	3	—	—	—	—	—	—	104	43.6
Fegen	Nov. 54	—	—	—	2	1	2	12	16	29	17	12	4	3	1	1	—	—	—	—	100	45.2
Flåren	Nov. 52	—	—	—	1	3	2	—	1	1	—	—	—	—	—	—	—	—	—	—	8	42.0
Åsnen	Nov. 51	—	2	1	1	5	8	10	12	6	3	2	1	—	—	—	—	—	—	—	51	43.2
Ivösjön	Dec. 55	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	2	—
Vombsjön	Dec. 53	—	—	2	4	3	3	3	4	3	—	—	—	—	—	—	—	—	—	—	22	42.1

Total: 2.840 specimens

Laxen och klimatet

Av Gunnar Svärdson

Innehåll

1. Inledning

Laxen, *Salmo salar,* har på senare år ådragit sig en betydande uppmärksamhet. Förklaringen härtill är denna fisks stora ekonomiska betydelse för fiskarebefolkningen längs den svenska ostkusten och den roll arten spelar i avvägningsfrågorna vid kraftverksbyggena. Kraftverksindustrin bekostar också för närvarande omfattande undersökningar, som tar sikte på möjligheterna att med uppfödningar producera utvandringsmogna laxungar (smolts) och därmed kringgå älvstadiet i laxens liv.

Men även ur biologisk synpunkt erbjuder laxen många intressanta problem. De sammanhänger främst med den egendomliga dubbla biotop som laxen har, då den ju tillbringar de första åren av sitt liv i älvarna, och därefter några år som snabbt tillväxande fisk ute i hav eller stora insjöar t.ex. Vänern.

De många fakta om laxens liv samt de talrika avkastningssiffror som framkommit, accentuerar behovet av en överblick och en analys av de stora populationsväxlingar, som laxen i Östersjön uppvisat under de senaste 70—80 åren. Lindroth (1950) och Svärdson (1955) har gjort sådana sammanställningar.

Det senare arbetet har ådragit sig stark kritik av Lindroth (1957). Den framförda kritiken bygger enligt min mening på grava missförstånd och det är därför angeläget att bemöta den. Samtidigt blir detta ett tillfälle att redovisa det väsentliga innehållet i de hypoteser om primär- och sekundärfluktuationens natur, som de utförda undersökningarna lett fram till.

De uppställda hypoteserna har mycket betydande praktiska konsekvenser.

2. Existensen av rika och fattiga smoltklasser

Det är vanligt att fiskbestånd byggs upp av årsklasser, som starkt skiftar i individantal. Utforskningen av hur dylika rika eller fattiga årsklasser uppkommer, pågår i många länder. För närvarande kan man väl säga så mycket att man allmänt antar att årsklasserna dimensioneras tidigt och att näringsförhållandena och predatorerna därvid antas vara de viktigaste orsakerna.

I min tidigare artikel (SVÄRDSON 1955) antog jag att de mindre fluktuationerna i laxfiskets utfall i älvarna till stor del berodde på en växling mellan rika och fattiga smoltklasser. Dessa skilde sig från årsklasserna därigenom att de omfattade en samling olikåldriga laxungar, som alla en viss vår genomgick den hormonella omvandling som smoltifikationen utgör.

Smoltklassernas storlek sammanhängde i sin tur med vintrarnas isläggning. Detta innebar att en rik smoltklass uppstod den vår och försommar som följde på en mild isvinter, medan en fattig smoltklass på motsvarande sätt uppstod sådana vårar då föregående vinter haft en betydande isläggning. Uppgifterna om Östersjöns isläggning kom från JURVA (1952), vars arbete stimulerat mig till studiet av laxfluktuationernas detaljer.

Medlemmarna av en smoltklass ger sig visserligen ut från älven ungefär samtidigt, dvs samma säsong, men de återkommer inte till älven alla på en gång. Några återvänder redan nästa sommar (grilse), ytterligare en grupp av då tyngre fiskar kommer tillbaka två år efter utvandringen, en majoritet av tunga fiskar kommer efter tre år, en mindre grupp av mycket tunga fiskar kommer tillbaka först efter fyra år och några få exemplar kan dröja sig kvar i havet ytterligare ett år. Dessa, de sista, återkommer alltså år 5, om den vinter, vars isläggning studerats, anges som år 0. (Alla årsangivelser förutsätter att som vinter enbart räknas den period som infaller efter nyår).

En rik smoltklass bör därför ge en ökning i älvens fångst efter två-tre år. Vilket år som blir det bästa beror på flera omständigheter, som senare skall diskuteras i detalj. En fattig smoltklass bör i analogi härmed ge en nedgång i älvfångsterna under de fyra-fem år som smoltklassen existerar. Nedgången blir mest markerad år 3 och återhämtas igen år 4 och framför allt år 5, då ju smoltklassen praktiskt taget är borta ur fångsterna.

En rik smoltklass kommer därför i en rad årssiffror över fångst i älvarna att ge sig tillkänna som en fångsttopp 2—3 år efter det år då smoltklassen dimensionerats, medan den dåliga smoltklassen ger sig tillkänna som en sänkning och därefter en skenbar topp 4—6 år efter det klass-skapande året. Toppen är i detta senare fall endast skenbar, då den ju egentligen bara innebär en återgång till utgångsläget, men efter de föregående årens lägre fångster framstår ju även en sådan återgång som något positivt, som en ökning.

Tabell 1. Laxfångst i kg vid Gäddvik, Lule älv, åren 1891—1956.

År	Efter 30 milda vintrar isläggning < 16 enheter	År	Efter 30 stränga vintrar isläggning > 16 enheter
0	7.744	0	6.271
1	7.426	1	6.496
2	7.820	2	6.199
3	6.800	3	7.208
4	5.430	4	8.350
5	5.624	5	8.056
6	6.859	6	6.664

De fakta som övertygade mig om existensen av rika och fattiga smoltklasser var följande:

1. En lång rad uppgifter från in- och utland om fångster under olika år, blev, när de sattes i relation till kända meteorologiska förhållanden och isvintrar, sammantagna ett mycket starkt indicium på att fångstökningar tenderade att inträffa 2—3 år efter milda vintrar och 4—6 år, oftast 5 år, efter kalla.

2. Det svenska laxfiske, som har den längsta oavbrutna statistikserien, Svartö laxfiske i Lule älv, uppvisade en stark fångstökning 1808—09 efter de stränga vintrarna 1803—1805. Rekordfångsten i den 150-åriga serien, år 1826, kom efter den mycket stränga vintern 1821, som i sin tur omedelbart följdes av en rekordmässigt varm vinter, nämligen 1822.

3. För perioden 1830—1950 kunde fångstsiffrorna i Svartöfisket sättas i direkt relation till de värden över Östersjöns isläggning som Jurva publicerat. Därvid befanns att en ökning i fångsterna tenderade att inträffa 2—3 år efter de mildaste vintrarna och likaledes en fångstökning 4—5 år efter de strängaste vintrarna.

En variansanalys visade att de i Svartöfisket funna olikheterna i fångst åren efter vintrar av olika stränghet sannolikt var reella. Visserligen var förutsättningarna för användning av variansanalys ingalunda idealiska, eftersom de ingående fångstsiffrorna varken var helt oberoende av varandra (varje biologiskt verkade faktor skulle ju ge utslag i fångstsiffrorna under flera på varandra följande år) eller oberoende av den stora fluktuation som innebär att perioder av stränga vintrar ger ökad laxfångst.

I detta speciella fall var dock de funna olikheterna sådana att de mycket starkt indicerade en verklig biologisk realitet. En diskussion om de statistiska metodernas brister ansågs ligga utanför artikelns omfång, särskilt som beräkningarna på Svartömaterialet endast utgjorde en del av den stora indiciebörda som pekade på att rika och fattiga smoltklasser var en realitet.

Genom vänligt tillmötesgående av Herr Sven A. Hedström, Gäddvik, är jag nu i tillfälle att för laxfisket Gäddvik i Lule älv ge en kompletterande analys av fångsternas fluktuation där åren 1891—1956, sett i relation till vintrarnas stränghet (tabell 1).

Tabell 2. Laxfångst i kg vid Norrfors, Ume älv åren 1887—1924.

År	Efter 14 milda vintrar isläggning < 16 enheter	År	Efter 18 stränga vintrar isläggning > 16 enheter
0	3.567	0	3.630
1	3.083	1	4.061
2	3.619	2	3.722
3	3.191	3	4.026
4	3.792	4	3.873
5	3.683	5	4.497
6	3.616	6	4.832

Av tabell 1 framgår att Gäddviks laxfiske utvisar en topp andra året efter en mild vinter och likaledes en topp 4—5 år efter en sträng vinter.

I samband med utredningen rörande det bekanta Stornorrfors-målet i Ume älv har vidare fiskeriintendent Sten Berg presenterat en svit avkastningssiffror från Norrfors laxfiske. De gäller åren 1887—1924 och sammanställs ovan (tabell 2) i relation till vinterstränghet.

Norrfors-materialet är litet och slumpvariationen som följd därav stor. Intressant är att trots detta en markerad fångstökning föreligger för åren 5—6 efter de stränga vintrarna och att i varje fall en tendens till ökning föreligger för år 2 efter en mild vinter.

Lindroths *kritik*. Lindroth anser de av mig funna fångsttopparna vissa år efter olika stränga vintrar vara artefakter, framkomna genom att några rikligt givande laxår i Svartöfisket råkat infalla 2—3 år efter en mild vinter, respektive 4—6 år efter en sträng. De skulle i själva verket vara åstadkomna av den primära, dvs den storvågiga fluktuationen.

Det är självfallet riktigt att både primär- och sekundärfluktuationen påverkar de enskilda årens fångstsiffror. Men — och detta är en svaghet i Lindroths kritik — han har aldrig insett att de bägge fluktuationerna är motsatt beroende av en sträng vinter. Därav följer, som senare skall diskuteras i detalj, att den mindre fluktuationen uppträder som en störning på den större, men just därigenom blir möjlig att studera.

Lindroth gör en mycket värdefull uppdelning av Svartömaterialet i en högfångst- och en lågfångstperiod (tabell 3).

Han menar nu att uppdelningen av materialet icke ger stöd för de slutsatser som möjligen kunde dragas av det samlade materialet, dvs de av mig redovisade slutsatserna. Vad uppdelningen visar är dock att smoltklassväxlingarna framträder med en rent schematisk tydlighet under högfångstperioden och att de är mycket svagare under den period då laxfångsterna i Svartö varit låga.

Vad orsaken än må vara till detta, så är det intressant att finna att det icke kan bero på att, som Lindroth antyder, Svartö-materialet skulle vara otypiskt för Lule älv, eftersom topparna, som ovan visats, föreligger i Gäddviksmaterialet från samma älv.

Tabell 3. Laxfångster vid Svartö, deciton, uppdelade på hög- och lågfångstperioder.

Efter	Högfångstperiod 1835—1900		Lågfångstperiod 1901—1951	
år	Milda vintrar	Stränga vintrar	Milda vintrar	Stränga vintrar
0	9.9	9.9	1.9	1.5
1	9.3	10.3	1.8	2.0
2	11.8	8.3	1.8	1.6
3	11.2	9.8	1.7	2.1
4	9.0	9.9	1.5	2.7
5	8.7	10.6	1.7	2.2
6	8.9	10.2	1.8	2.3

Det kan inte heller vara så att, som LINDROTH tror, smoltklass-fluktuationerna är en artefakt, beroende på att några rikt givande år under högfångstperioden givit så starka utslag, eftersom de finns i materialet från Gäddvik och Norrfors, vilka bägge hänför sig till den period som Lindroth med rätta karakteriserar som en lågfångstperiod.

Tämligen utförligt diskuterar LINDROTH de statistiska metodernas bristande användbarhet i ett fall som detta. Med den presentation han ger frågan förefaller uppgiften onekligen nära nog olöslig, men eftersom jag trots dessa svårigheter fått fram sekundärfluktuationen kan en förklaring vara på sin plats. Det beror icke på att jag företagit en variansanalys — medan LINDROTH tror den vara en korrelationsberäkning — utan på att de framkomna värdena stödde varandra ömsesidigt.

De metodiska svagheterna uppvägdes av det faktum att fångsttopparna 2 respektive 3 år efter en mild vinter visserligen var för sig redan var på gränsen till signifikans, men att de tillhopa starkt indicerade en biologisk realitet, som bl.a. fordrade att dessa bägge värden skulle vara avvikande i samma riktning. Än starkare blev denna sannolikhet — tyvärr omätbart — då de framkomna topparna 4 och 5 år efter den stränga vintern, på motsvarande sätt, inte bara stödde varandra utan även de två värdena från mildvinterns följder. Alla lät sig ju enhetligt förklaras och tillhopa utgjorde de en betryggande sannolikhet för att slumpen ej åstadkommit resultatet.

När till detta lades övriga indicier, som i och för sig var mycket starka, var det ganska naturligt att realiteten av fenomenet inte gärna kunde betvivlas. Dessa övriga, icke-statistiskt behandlade indicier, utelämnas helt av LINDROTH då han söker förneka existensen av de fångst-toppar efter olika stränga vintrar som av mig påvisats.

Sekundärfluktuationen i form av smoltklasser kan alltså inte gärna betvivlas och i ett senare avsnitt demonstreras att den icke blott gäller för Lule och Ume älvar utan för hela den svenska laxstatistik från älvarna som ingår i den av LINDROTH (1950) ritade s.k. laxkurvan.

3. Uppkomsten av smoltklasserna

De mångåriga undersökningarna vid Cultus Lake, British Columbia har klart visat bl.a. att större laxungar har bättre överlevnad än mindre ungar. Det gäller här sockeye salmon (*Oncorhynchus nerka*) och ur FOERSTERS (1954) senaste arbete kan, genom interpolering från hans fig. 4, p. 346, följande förbättring i överlevnaden tabelleras (tabell 4).

Tabell 4. Laxungarnas överlevnad i relation till storlek vid utvandringen.

Storlek, cm	Procent överlevnad till adult	Storlek, cm	Procent överlevnad till adult
6	0.5	9	2.2
7	0.8	10	3.8
8	1.4	11	6.0

Samma princip gäller tydligen även för den atlantiska laxen. CARLIN (1955) konstaterade bättre överlevnad hos större ungar och utsättning i havet av överåriga, i dammar kvarhållna laxar, har gett sensationellt höga återfångster, av storleksordningen 30 %.

Naturlig mortalitet kan hänföras till de tre grupperna av orsaker: näringsbrist, sjukdomar och fiender (predatorer). Den utvandringsmogna laxungen torde främst hotas av predatorer, ehuru näringsbrist möjligen kan råda under en övergångsperiod, innan den unga laxen helt övergått till sitt i havet pelagiska, jagande levnadssätt.

Fiskars tillväxt är positivt beroende av temperaturen. Varma försomrar har på senare år i en rad fall (jmf. t.ex. SVÄRDSON 1951, 1957) bevisats medföra förbättrad tillväxt hos fiskar. Efter en mild vinter med ringa isbeläggning kan havet uppvärmas snabbare än eljest. Milda vintrar betyder således ett om våren relativt varmt hav.

En laxunges tillväxt i havet bör därför vara beroende av vinterns, dvs i detta fall egentligen vårens, vattentemperatur. En varm vår ger snabbare tillväxt och därigenom en minskad risktid, dvs en minskad dödlighet. Omvänt ger en kall vår en fördröjd tillväxt, en förlängd period under vilken laxungen kan övermannas av fiender, och därmed en ökad mortalitet.

Det är alltså fullt i överensstämmelse med redan väl kända fakta att förutsätta att kalla vårar ger dåliga smoltklasser, milda vårar däremot rika smoltklasser.

Detta är sannolikt den yttersta, den ultimala, faktorn bakom rika och fattiga smoltklasser efter olika typer av vintrar. Men modern ekologisk forskning har visat att man ofta får räkna med både ultimal och proximal orsak i naturen.

Med proximal faktor menas då den stimulus som normalt utlöser en reaktion hos vilda djur, varigenom de kommer att företa sig något ändamålsenligt »i god tid». Flyttfåglarna ger sig av före vinterns näringsbrist och igelkotten börjar sin vintersömn innan det är »nödvändigt». Genom urval har reaktioner framkommit på proximala faktorer som »varnar» djuren i god tid.

För att en proximal faktor skall kunna utbildas måste den sammanfalla med den ultimala i så måtto, att dess »varning» går åt rätt håll. Om laxungar löper risk att utsättas för större dödlighet under sådana år då havet är kallt, borde genom naturligt urval en reaktion på en proximal faktor kunnat uppstå, som fick dem att en sådan kall vår hellre till nästa år uppskjuta sin omvandling till smolt.

I min tidigare artikel uppehöll jag mig relativt kortfattat vid den ultimala faktorn (sid. 250) men desto mer vid den proximala orsaken (245—250) till det som jag antog vara en regel »It seems rather probable that a warm spring accelerates the transformation of smolts, giving a good smolt class and, conversely, a cold spring or summer gives a subnormal transformation and a bad smolt class» p. 242).

Jag fann nämligen att en rad dittills mycket gåtfulla förhållanden kunde få en enhetlig och tillfredsställande biologisk förklaring om man antog:

1) närvaron av en kritisk period under vilken det avgjordes om den hormonella omvandling som könsmognad och utvandringsmognad utgör, skulle igångsättas ett visst år eller ej,

2) att tröskelvärdet för en sådan omvandling sänktes med stigande fysiologisk ålder (ålder×storlek) och att könsolikheter förelåg, samt

3) att en omvärldsfaktor, i första hand en temperaturändring, som inträdde under den kritiska perioden, var en utlösande stimulans.

Med dessa enkla antaganden (jmf. Svärdson 1956 a) kunde man ge en rimlig förklaring till en rad gåtfulla fenomen: laxungarnas i nordligare älvar allt högre ålder och större kroppslängd vid utvandringsmognaden, uppkomsten av det i den norska älven Namsen levande stationära laxbeståndet som ej vandrar till havs, det egendomliga förhållandet att laxhanar leker redan före utvandringen till havet, hanarnas större tendens att återvända tidigt och därmed utgöra huvudmassan av grilse, artskillnaden mellan lax och öring, varvid den senare är mera trög att mogna till utvandring, de lokalt starkt skiftande vanorna i olika öringbestånd, de egendomliga skillnaderna hos ålen beträffande hanars och honors geografiska fördelning samt ålhonornas långvariga kvarblivande, och stora kroppslängd, i nordliga vattensystem.

Lindroths *kritik*: Efter lång diskussion och jämförelse med kända mätningar använde jag de av Jurva publicerade isvärdena som relativa mått på vårens klimat, i första hand på havets allmänna temperatur under vårmånaderna. Jurvas värden går tillbaka till 1830 medan temperaturmätningar bara finns för relativt få år i senare tid, helt saknas för några av krigsåren samt slutligen är olämpliga för snabba jämförelser eftersom de är starkt beroende av vilka fyrskepp och djuplägen man väljer. Gentemot de av mig valda isvärdena föredrar LINDROTH däremot temperaturmätningarna som han anser överlägsna.

Jag antog vidare att även älvarnas vattentemperatur — om vilken likaledes endast relativt få direkta uppgifter föreligger — i stort sett följde det allmänna vårklimatet, dvs följde Östersjöns avkylning under vintern. Här har emellertid LINDROTH med siffror visat att någon sådan korrelation kanske ej föreligger i Indalsälven. Om detta verkligen är riktigt skulle det innebära att älvtemperaturen är oberoende av Östersjöns allmänna värmeförlust under vintern och därmed skulle möjligheterna att laxungarna utbildat en reaktion på en proximal »varnande» faktor vara uteslutna eller i vart fall mycket försvårade.

Gärna medger jag att LINDROTHs siffror förvånat mig och att en diskussion av älvtemperaturen skulle ha stärkt min tidigare framställning. Ehuru frågan om laxungarnas proximala stimulus därmed kommit i ett delvis annat läge, betyder detta för huvudfrågan — laxbeståndets fluktuationer — självfallet bara att orsaken till smoltklassernas dimensionering i stället tenderar att läggas över på den ultimala faktorn, dvs den som verkar vid älvmynningarna.

Huvudtanken att fattiga smoltklasser utbildas vid kalla vårar i havet, rika smoltklasser däremot under varma vårar är helt opåverkad, även om det mot förmodan skulle visa sig att smoltifikationen är oberoende av sådana i älven märkbara stimuli som sammanfaller med havets temperatur. Definitionen av en smoltklass bör kanske också för tydlighetens skull ändras till att beteckna alla de laxungar som en viss säsong genomgår sin hormonella omvandling, vandra till havet och där lyckligen påbörja sitt pelagiska liv.

Om smoltifikationen verkligen kan bevisas vara helt oberoende av havstemperaturen, så skulle detta framstå som ett märkligt exempel på bristande anpassning hos laxungarna.

4. Laxuppvandringens temperaturberoende

Kunskapen om den tid laxen tillbringar i havet vilar på tolkningar av laxfjäll, tagna på laxar som fångats i älvarna på uppgång för lek. I svenska östersjöälvar har sådana bestämningar utförts av ALM och ROSÉN på sammanlagt 3.737 laxar och i Finland har JÄRVI undersökt icke mindre än 29.436 laxar (data sammanfattade hos SVÄRDSON 1955).

För en fruktbar diskussion av laxuppvandringens temperaturberoende måste man veta hur en normal, dvs en genomsnittlig uppgång ter sig. Översiktliga data har samlats i tabell 5.

Olikheten mellan de svenska och finska undersökningarnas resultat är relativt obetydlig. Det föreligger en markerad geografisk variation för den tid laxen tillbringar i havet, varvid generellt sett laxen stannar flera år i havet om detta är kallt än om det är varmt (SVÄRDSON 1955, sammanfattning). Inom Östersjöområdet är denna geografiska variation relativt obetydlig, Tabell 5. Data om havsår, vikt mm på i älvarna nystigna laxar.

	Havsår					
	1	2	3	4	5	Totalt
Medelvikt (Järvi) kg	1.6	5.7	11.5	16.4	20.2	
Procent laxar (Sverige)	5	27	61	7	—	100
Vikt i fångst, kg	8	154	702	115	—	979
Procent laxar (Finland)	10	27	53	9	1	100
Vikt i fångst, kg	16	154	610	148	20	948

främst beroende på att laxarna tycks uppsöka samma uppväxtområden i södra Östersjön och att de därigenom utsätts för mycket likartade temperaturpåverkningar. En viss tendens till kortare havsvistelse finns dock i de nordligaste älvarnas, främst i Torne älvs laxbestånd, beroende på att laxungarna kvarstanna mycket länge i denna älv och därför ha stark tendens att snart återvända. Även denna regel gäller generellt för laxen.

Laxens tillväxthastighet spelar naturligtvis en stor roll för längden av den period den tillbringar i havet. Ju varmare havet är, desto snabbare växer laxen och desto tidigare har den nått sådan mognad att könsmognaden kan inträda och utlösa uppvandring i älv. Järvi (1948) fann att de laxar som fångades åren 1942—1944 var väsentligt kortare och lättare — i förhållande till längden av sin havsvistelse — än laxar som fångats under de föregående tjugo åren. Det var uppenbarligen den låga temperatur som Östersjön hade i samband med de stränga vintrarna, som orsakat denna dåliga tillväxt. Järvi antar själv som alternativ att det kunde ha berott på näringskonkurrens genom att laxbeståndet ökat men denna förklaring är osannolik, dels beroende på den rika näringstillgången för lax i havet, dels, och framför allt, därför att den stora ökningen i laxbeståndet började först med 1943 års smoltklass, som senare skall visas.

En rik smoltklass skulle, som framgår av tabell 5, leda till en kraftig ökning av laxfångsten framför allt efter 3 år, då den stora mängden laxar återvänder. Men så enkelt blir det inte, eftersom den varma vår, som ger en rik smoltklass, också åstadkommer en allmän acceleration av laxarnas tillväxt och utövar en direkt påskyndande effekt på uppgången.

Det har klart visats (Jacobsen och Johansen 1921, Alm 1924) att laxuppgången stimuleras av en varm försommar. Det innebär att lekklassernas dimensionering, liksom smoltklassernas, är temperaturberoende och gynnas av värme. På analogt sätt försenas uppgången av kyla och den kalla vår som ger en fattig smoltklass medför också samtidigt en generell fördröjning av havsvistelsen för utegående laxar.

Den dubbla effekten av vårtemperaturen på smoltklasser och lekklasser gör det vanskligt att dra en gräns och säga att så mycket av fångstökningen beror på den rika smoltklassen och så mycket på värmens acceleration av uppgången och tillväxten i havet (därmed på nästa års uppgång). Det är instruktivt att se nettoresultatet av dessa bägge inflytanden på de schematiskt tydliga klimateffekter, som Svartöfisket uppvisar för 1800-talet, dvs den period då laxbeståndet var stort (och de fåtaliga tumlarna i Östersjön accentuerade växlingen av smolt- och lekklasser).

	År						
	0	1	2	3	4	5	6
Efter en mild vinter	9.9	9.3	11.8	11.2	9.0	8.7	8.9
Efter en sträng vinter	9.9	10.3	8.3	9.8	9.9	10.6	10.2

Den höga fångst som den rika smoltklassen vid en varm vår borde ge år 3 finns där visserligen men har »stjälpts framåt» så att ett ännu högre fångstvärde uppnåtts år 2. Men även år 1 och år 0 (som ju borde ha en rik lekklass) har högre fångster än åren 4—6. Vi ser alltså att den rika smoltklassen visserligen dominerar bilden men att förkortningen av havsvistelsen också haft en påtaglig inverkan.

Efter den stränga vintern borde den dåliga smoltklassen haft sitt första negativa inflytande år 1 medan fångsten år 0 varit opåverkad. Men fördröjningen som den kalla våren åstadkommit på uppvandringen år 0 har uppvägt den väntade fångstminskningen år 1 och uppskjutit inverkan av den dåliga smoltklassen till år 2. Först med år 5 har sedan denna effekt övervunnits och vi får den väntade toppen.

Det var vid mina studier av denna dubbla klimatpåverkan på smolt- och lekklasser snart uppenbart att en närmare analys av vardera faktorns enskilda inflytande helt och hållet var beroende av hur pass tillförlitlig vår kännedom om laxens havsvistelse var. Jag kom därvid att kritiskt pröva basen för denna kunskap, dvs de utförda fjälltolkningarna.

Därvid befanns snart att en rad tveksamma punkter förelåg, som omöjliggjorde en fortsatt analys förrän större klarhet vunnits om tillförlitligheten av de gjorda fjälltolkningarna. Tveksamheten gällde följande punkter:

1. Fjällprovens representativa insamlande. Det var av största vikt att veta att ingen som helst selektion företagits, så att fjäll tagits t.ex. i mindre utsträckning av stora än av små laxar. Varje sådan selektion, som ju mycket lätt kunde ha inträffat vid ett praktiskt fiske, där det är besvärligt att handskas med stora fiskar, påverkade modellerna på det mest allvarliga sätt.

2. Olofsson (1932) hade påvisat att smålaxar vid norrlandskusten den svala sommaren 1931 ej påbörjat sin tillväxt i havet förrän under senare hälften av juni. Eftersom uppgången började redan i maj, kunde man mycket väl tänka sig att i början av juni fångade laxar fått sin yttersta tillväxtzon på fjällen felaktigt hänförd till år 1931, dvs uppgångsåret medan det i själva verket skulle gälla 1930, dvs föregående år. Samma allvarliga möjlighet till feltolkningar har visat sig vara en realitet vid fjällundersökningar på andra fiskar vid Sötvattenslaboratoriet. Konsekvensen för en årsklassmodell blir att ett fel på ett kalenderår kan gälla de mindre laxarnas antagna havsvistelse.

Tabell 6. Laxuppvandringen, procentuell fördelning, under olika årstider.

	mars	april	maj	juni	juli	augusti	september	oktober
Torne älv	—	—	—	24.7	74.0	1.3	—	—
Ume älv	—	—	—	40.9	55.0	3.9	0.2	—
Dalälven	—	—	23.0	63.5	12.0	1.2	—	—
Mörrumsån	0.7	5.7	35.2	34.6	16.1	4.7	1.4	1.6

3. JÄRVI och MENZIES (1936), sin tids mest erfarna laxfjälltolkare, hade särskilt påpekat att vissa fjäll uppvisade en »check» under första året av havsliv. De underströk särskilt att det i många fall var svårt att avgöra om laxen tillbringat denna del av sitt liv i havet eller i älvmynningen. Till detta kunde läggas erfarenheter av märkta laxungar, under 1950-talet, som i flera fall icke lämnat kusten på ett år. En möjlighet till feltolkning på ett helt kalenderår förelåg uppenbarligen även här.

4. De stora laxarna bereder också vissa problem, beroende på den snäva årstid som laxuppgången har norrut, jämfört med sydligare älvar. Data härom återfinns, efter ALM (1934) i tabell 6.

Denna översikt torde väl ganska klart visa att uppgången av lax i nordligare älvar är säsongmässigt begränsad, sannolikt av faktorer som har med klimatet, t.ex. temperaturen att göra. Anmärkningsvärt är bl.a. att större delen av uppgången äger rum under en tid, då älvarna på det hela taget är varmare än havet. Lång tid återstår då ännu innan laxen skall leka. NORDQVIST (1906) citerar norska uppgifter om att laxen stiger 2—4 veckor senare i älvar med mycket glaciärvatten, vilket tolkats som beroende på dessa älvars låga temperatur. Man får det allmänna intrycket att laxarna söker sig upp i älvarna så fort det är dem möjligt och att de är »beredda» så fort de rätta stimulanserna (bl.a. högvatten) infinner sig.

En stor lax har ingen +zon (dvs smal yttre tillväxtzon) på sina fjäll och man antar därför att den icke vuxit något under den sommar uppvandringen sker. Men om laxen, som tillbringat några år nere i södra Östersjön, kommer för »sent» till en nordlig älv, dvs först i senare hälften av augusti, vad händer då? Visserligen kan en och annan nystigen lax visa sig i nordliga älvar även om hösten. I Kemi älv kallas sådana laxar »juominki» (NORDQVIST 1906). Men det är å andra sidan sannolikt att de är flera i sydligare älvar. Beror nu detta på att flera kommer »för sent» i sydligare älvar eller är skillnaden skenbar, genom att några laxar stannar över vintern vid kusten längst i norr? Det senare alternativet är en klar möjlighet.

De många tänkbara orsakerna till diskrepans mellan den verkliga tid laxar levat i havet och den bild därav vi på basis av fjällproven har, påverkar högst avsevärt en närmare analys av hur en viss vår påverkar smoltklassen, jämfört med lekklassen. Nästan varje enskild lax i de högre viktgrupperna, som flyttas över i modellen från antagen återkomst ena året till det andra, inverkar på bedömningen.

Med hänsyn till dessa vanskligheter avstod jag i min tidigare artikel från publicering av de många modeller jag gjort upp för olika alternativ utan nöjde mig istället med en hänvisning till att de funna fångsttopparna mycket väl lät sig förklaras och uppmanade i stället till att de talrika laxfjäll som på senare år insamlats på fiskar, vars havsvistelse på grund av djurets markering är känd, snarast måtte studeras så att tveksamheterna på denna punkt kunde undanröjas.

LINDROTHS *kritik.* Mina antaganden om hur laxfjällen kunde bli feltolkade har ådragit sig LINDROTHS uppmärksamhet. Möjligheten att laxen kom för sent och väntade över vintern vid kusten avfärdas som ett fullkomligt osannolikt antagande.. Likaså vill LINDROTH, med hänvisning till sin erfarenhet från Indalsälven, ej hålla med om att laxuppgången slutar i augusti.

Värre är att LINDROTH trott det vara nödvändigt för mig att underkänna fjällproven helt för att få smoltklasserna att stämma med fångsttopparna. Han har ej tänkt på att det är just levnaden i havet under normalt högst fyra år som konstituerar möjligheten för att en *dålig smoltklass* ger en *fångsttopp efter fem år.* Han har i stället trott mig anta att den dåliga smoltklassen var rik på individer, som alla var ute i havet fem år och därvid åstadkom toppen när de återkom.

Det är mycket beklagligt att jag ej ännu tydligare i min artikel klarlade varför jag betraktade fjällproven med en viss skepsis, dvs att denna fråga bara berörde särskiljandet av vårklimatets inverkan på smolt- och lekklassernas del i fångsttopparna. LINDROTHS missförstånd hade väl ändå icke behövt ske, ifall han bara läst min artikel med den eftertanke, som de tämligen invecklade sammanhangen kräver. Den kritiska grundinställning till mina synpunkter och min artikel som går i dagen i — lika oberättigade — anmärkningar mot citat, diagram mm. har tydligen helt skymt sikten för de onekligen mer viktiga principfrågorna.

5. Korrelationen mellan stränga vintrar och goda laxfångster

Laxbeståndet är underkastat både smärre och större fluktuationer. De mindre fluktuationerna beror sannolikt, som framgått av det föregående, i första hand på växlingen av rika och fattiga smoltklasser och den modifikation i fångsterna som olika starka lekklasser medför. Klimatet är i bägge fallen den verksamma faktorn.

Eftersom stränga vintrar ger dåliga smoltklasser, borde följaktligen tidsperioder då stränga vintrar uppträder tätare, utmärkas av dåligt laxfiske, medan tvärtom perioder med milda vintrar borde ge höga laxfångster. Men det egendomliga är att motsatsen inträffar. Den stora primärfluktuationen inom laxbeståndet är, som alla nu är eniga om, beroende av vinterstränghet, men på sådant sätt att *stränga vintrar utmärker sådana tidsperioder då laxfångsterna ligger högt.*

Detta förefaller i förstone paradoxalt, men är i själva verket ganska enkelt. Primär- och sekundärfluktuationen *verkar bägge med vinterklimatet som förmedlare, men i olika riktning, därför att de bakomliggande biologiska faktorerna är helt olika.*

En så sträng vinter att en betydande del av Östersjön blir isbelagd, undanröjer tydligtvis ett annars övermäktigt hinder för uppkomsten av ett rikt laxbestånd. Visserligen åstadkommer den stränga vintern med efterföljande kalla vår en dålig smoltklass, som ger nedsatta fångster i älvfisket under de närmaste fyra, möjligen fem åren, men redan nästa vår kan å andra sidan ge en smoltklass som helt kan utnyttja de förbättrade överlevnadsmöjligheterna. Sannolikheten för en reell fångsttopp i älvarna efter 4—6 år blir stor.

När vi studerar korrelationen mellan stränga vintrar och god laxfångst i älvarna, bör vi alltså vänta oss en starkt positiv korrelation, men sitt högsta värde får koefficienten om is- och laxfångstvärden förskjutes inbördes med fem—sex år. Det blir samma förhållande som om vi skulle mäta höjden av en dyning, på vilken överlagrats småvågor gående i motsatt, alltså dämpande riktning. Först då vi mäter dyningen vid topparna på de överlagrade småvågorna får vi de högsta värdena på dyningens våghöjd.

I min tidigare artikel (SVÄRDSON 1955) fann jag en starkt signifikant korrelation mellan vinterstränghet och goda laxfångster om en förskjutning på fem år gjordes mellan is- och laxvärdena. LINDROTH (1957) har nu gått vidare och undersökt nio olika förskjutningslägen mellan de bägge sifferserierna. Han finner att samtliga lägen ger en signifikant korrelation men att de allra högsta värdena ernås just vid fem—sex års förskjutning. Därmed har LINDROTH följaktligen visat inte bara att rika laxfångster tenderar att uppträda under perioder av stränga vintrar utan även att en sekundärfluktuation i motsatt riktning utmärker hela den svenska laxstatistiken från älvarna.

LINDROTHS *kritik.* Vid sina studier av skrakarnas predation på laxungar i Indalsälven har LINDROTH (1955) funnit att dessa fåglar förtärde uppskattningsvis omkring 350.000 laxungar i älven under tiden juni—september. Med hänvisning till överensstämmelsen mellan isvintrar och goda laxfångster, via sälar eller tumlare, finner han därvid att även skrakarna kunde bidra till en sådan biologisk förklaring. Följdriktigt förklarar han »skrakens efterhållande i de återstående laxälvarna vara ett första rangens fiskeriintresse» (LINDROTH 1955 b).

LINDROTH har ej insett att primär- och sekundärfluktuationen — sådana jag förklarat dem — har motsatta beroenden av vintrarna. Deras samverkan leder därmed till en karakteristisk försening i laxbeståndets ökning. I sin kritik (1957) hänvisar han därför till den försenade ökningen av laxbeståndet på 40-talet efter den bevisade tumlardöden 1940, likaså till den samtidiga toppen i Klarälven och menar detta snarare kunna tyda på att det är under älvlivet som laxen är känslig för de stränga vintrarnas konsekvenser.

Det är härav tydligt att LINDROTH icke kunnat frigöra sig från tanken att skrakarna eller någon annan på älvstadiet verkande laxfiende utgör den faktor som skapar primärfluktuationen. I själva verket är dock sekundärfluktuationens natur sådan, att den inte bara förklarar den försening i laxbeståndets ökning som förvånar LINDROTH, utan även omöjliggör tanken på att den primära fluktuationen kan skapas av någon på älvstadiet verkande faktor. Detta skall utförligt visas i nästa avsnitt.

6. Den primära fluktuationens orsak

Laxfångsten i de svenska älvarna låg högt under senare delen av 1800-talet, började hastigt sjunka under 1890-talet och nådde ett minimum i början av 1900-talet. En viss återhämtning förekom omkring 1920, därefter följde en ny nedgång under 1930-talet varpå den mycket kraftiga uppgången på 1940-talet förde laxfångsterna upp till samma höga värden som de haft under 1800-talets senare del.

Nedgången i laxfångsterna under 1890-talet och början av detta sekel tolkades då allmänt som resultatet av flottning och sedermera kraftverksbyggnaders negativa inverkan. Direkta undersökningar över flottningens verkan stödde dock ej denna tanke och den kraftiga höjningen av fångsterna under 1940-talet visade eftertryckligt att ej heller kraftverken kunde förklara den stora primära fluktuationen. Ingen var laxfiskets »stora faktor».

Fiskodling ansågs av sina mest entusiastiska utövare kunna ge en förklaring till 40-talets sensationella uppgång men vid närmare eftertanke kunde hypotesen omöjligt vara sannolik. Den dåtida fiskodlingen bestod mest i utsättning av nykläckt yngel och ingen ökning i denna verksamhet hade förekommit, i varje fall inte i sådan utsträckning att den på något sätt svarade mot ökningen i laxbeståndet. Dessutom gällde ökningen generellt alla älvar, oavsett om där hade utsatts yngel eller ej.

Några förespråkare hade även hypotesen om kraftverksregleringarna som positiva faktorer. Vattenståndet var ju numera, menade man, jämnare än förr och särskilt vintertid var vattnet icke så lågt som den naturliga avrinningen ibland kunde medföra. Därmed borde alltså laxynglets överlevnad förbättras, därför också beståndet kunna ökas. Många skäl talade emellertid mot att en sådan faktor, även om den kunde inverka, rimligen kunde ha så stor effekt.

Bättre grundad var då den hypotes, som ville se ökningen under 1940-talet som en följd av det under andra världskriget minskade fisket i Östersjön. Mot hypotesen talade dock, dels att ökningen i laxbeståndet var så stor och minskningen i fisket obetydlig, vidare det faktum att den branta nedgången av laxbeståndet på 1890-talet inte alls kunde bringas i samband med något just då ökat fiske i Östersjön. Om uppgången på 40-talet berodde på ändringar i fisket, så återstod ju ändå »den stora faktorn» när det gällde

90-talet. Sannolikare måste då självfallet vara att bägge berodde på samma, tillsvidare okända faktor.

Småningom koncentrerades hypotesbildningen kring de rent biologiska sammanhangen. De tre rekordstränga vintrarna 1940—1942 hade bevisligen åstadkommit stora förändringar i den terrestra faunan och det låg därför nära till hands att se även laxbeståndets ändring som en följd av dessa vintrar. Därvid måste man då förutsätta att en laxpredator, som i normala fall håller laxbeståndet nere, blivit så illa åtgången av vintrarna att laxbeståndet därför reagerat med sin våldsamma topp.

Antalet tänkbara laxfiender är ganska stort, eftersom man får räkna med möjligheten till påverkan på vilket stadium som helst av laxens liv. Ju tidigare i laxens livshistoria effekten satte in, desto större borde också de kvantitativa följderna bli.

Då sekundärfluktuationen, i form av dåliga smoltklasser vid stränga vintrar, nu blivit klarlagd, kan man emellertid sätta upp så många villkor, som en laxpredator måste uppfylla, för att kunna vara »den stora faktorn» att den långa listan på misstänkta djur hastigt krymper. Följande villkor måste vara uppfyllda:

1. Predatorn ifråga måste vara extremt känslig för stränga vintrar.

2. Djuret i fråga måste ha varit mycket fåtaligt under 1800-talets senare del, hastigt ökats i början av detta sekel och utsatts för stor decimering i början av 1940-talet.

3. En allmän ekologisk regel säger att predatorer oftast har ringa effekt på sitt bytesdjurs numerär. Bakgrunden till denna för lekmän ytterst förvånande huvudregel är att flertalet populationer har ett inre tryck (jmf. ERRINGTON 1956, SVÄRDSON 1956 b) i form av intraspecifik konkurrens och att den mortalitet som predatorer eller sjukdomar åstadkommer, därför oftast »fångas upp» av att den intraspecifika konkurrensen minskar. Laxen har knappast sådan intraspecifik konkurrens i havet, men väl i älven, där både utrymme och näring är begränsade. A priori kan därför sägas att det är osannolikt — ehuru inte uteslutet — att den stora faktorn, den bakom primärfluktuationen, kan finnas i älven. Eller om man formulerar dessa synpunkter som ett villkor: laxpredatorn måste verka på ett stadium då laxen har obetydlig intraspecifik konkurrens.

4. Sekundärfluktuationens växling mellan rika och fattiga smoltklasser var mycket markerad under 1800-talet, och är, ehuru mindre markerad, kvar ännu under 1900-talet. Detta innebär med andra ord att den primära fluktuationen icke förhindrat den sekundära.

Det fjärde villkoret skärper mycket starkt möjligheterna till deduktion. Tillämpat på skrakarna innebär det att de under 1800-talet skulle ha varit fåtaliga, sedermera talrikare, men hela tiden tillåtit utformningen av rika och fattiga smoltklasser. Under 1800-talet är detta rimligt, men hur skall man kunna tänka sig att de under 1900-talet dels varit talrikare, dels ändå växlat årligen så att de tillåtit utbildningen av fattiga smoltklasser efter stränga vintrar, rika smoltklasser efter milda? Skrakarna själva förutsättes ju vara känsliga för vintrarna och då borde de vara talrikare efter en mild vinter, alltså då åstadkomma stor predation och en dålig smoltklass!

Villkoret att primärfluktuationen inte undertrycker sekundärfluktuationen är i själva verket så strängt att enbart på detta villkor samtliga laxfiender verkande på laxens älvstadium i en enda grupp fritas från fortsatt misstanke. För alla gäller ju samma orimligheter som för skrakarna. När sedan de övriga villkoren tillkommer, främst nödvändigheten att djuret måste ha varit sparsamt under 1800-talets senare del och reducerats igen omkring 1940 så blir det fullt klart att inga laxfiender i älvarna är ansvariga för primärfluktuationen!

»Den stora faktorn» måste alltså finnas i havet. De förhållanden som påverkar smoltklassernas dimensionering verkar sannolikt — med den ultimala faktorn bakom smoltklasserna — i sista hand vid älvmynningarna och under laxens allra första tid i havet. Denna sekundärfluktuation är principiellt opåverkad av primärfluktuationen, som alltså bör inträda senare i laxens liv.

Detta innebär i sin tur att den primära fluktuationen bör uppstå genom en laxfiende som tar unglaxar, vilka redan vuxit ifrån sina »smoltfiender» längs kusten. Det finns bara några få djur som kan göra detta, främst sälar och tumlare, möjligen även stora torskar (som dock sannolikt ej är pelagiska som laxen).

Varken torsk eller säl är extremt känsliga för stränga vintrar och på sälarna stämmer inte villkor 2, dvs att djuren måste ha varit sparsamma under 1800-talet. Då var tvärtom enligt alla vittnesbörd sälarnas antal vida större än nu. Torskens frekvens på den tiden är föga känd.

Det finns veterligen bara ett enda djur som uppfyller alla de villkor man måste fordra för en förklaring till laxbeståndets primärfluktuation. Det är tumlaren, som är ytterst känslig för stränga vintrar, var sparsam under 1800-talets senare del och reducerades kraftigt år 1940.

Men det finns även direkta positiva indicier som pekar på tumlaren. Dess förmåga att ta fiskar är utomordentlig. Nyligen gjorda undersökningar (SCHEVILL and LAWRENCE 1956) på en annan tandval (*Tursiops*) — öresvinet — vid Woods Hole Oceanographic Institution visar att djuren har utmärkt syn både över och under vattnet, utomordentligt känslig hörsel samt en speciell förmåga till ekolokalisation av sina bytesfiskar. Tandvalen har ett knarrande läte då den jagar och genom ekot kan den »höra sig fram» till fisken, som den följaktligen kan ta även i rätt grumligt vatten. Det sistnämnda förvånade vid en nyligen gjord undersökning av vitvalens laxpredation i Alaska (Alaska Department of Fisheries. årsrapport för 1954) där det befanns att vitvalarna åstadkom förluster uppskattade till mellan 70.000 och 140.000 vuxna laxar (red salmon) bara inom ett ganska begränsat distrikt.

Tumlarens föda kan skattas till cirka 4 kg per dag. Tumlarna vandrar ut genom de danska bälten på senhösten för att återvända om våren, vilket uppenbarligen är en anpassning för att undgå kvävning av isen i Östersjön. Man vet alltså ej säkert hur länge de vistas i Östersjön — inte heller om alla vandrar ut normalt — men om man antar att de vistas i Östersjön 270 dagar per år, blir varje tumlares årliga fiskkonsumtion i detta hav drygt ett ton. Antar man vidare att en tumlares fiskdiet uteslutande består av smålax under en månads tid varje år och att de då äter till södra Östersjön relativt nykomna smålaxar på 100—200 gram, så innebär detta att varje tumlare kan förtära 1.000 smålaxar under denna korta tid. Men dessa smålaxar har vid det laget vuxit ifrån alla sina andra naturliga fiender och för fisket blir deras försvinnande nära nog en ren nettoförlust. Hade de fått leva några år skulle de, fördelade på havs- och älvfiske, representerat en potentiell fångst på 5.000—6.000 kg lax.[1]

Det kan vara av intresse att med direkta uppgifter om kända tumlarreduktioner kontrollera vad som hänt. Vi finner en häpnadsväckande överensstämmelse mellan tumlardöd och förbättrade fångster i fisket.

Tumlarna fångades förr i Lilla Bält vid Gamborg fjord, då de om senhösten vandrar ut ur Östersjön. Fångstsättet har nyligen beskrivits av MØHL-HANSEN (1954).

1880—1892 utövades denna fångst regelbundet varje säsong och ett medeltal av 1278 tumlare per år dödades (BEHRENDT 1929, LINDROTH 1957). När denna kraftiga årliga åderlåtning av tumlarbeståndet upphörde, skedde en ökning av tumlare i Bottenhavet (LING, se nedan).

När man betraktar den s.k. laxkurvan (LINDROTH 1950) finner man genast att just åren 1892—1893 utgör den vändpunkt, då det senare 1800-talets goda laxtillgång förbyttes i en kraftig och kontinuerlig nedgång, som på ett decennium skulle föra beståndet ner till sitt bottenvärde. Ej förrän ett halvt århundrade därefter, under 1940-talets toppår, återvann fångsterna den höjd de hade haft fram till 1890-talets första år.

1916—1919 återupptogs tillfälligt tumlarjakten vid Gamborg och under dessa år togs omkring 1.700 tumlare (LINDROTH 1957).

Laxfisket kring Gotland och vid Blekinge ökade starkt åren 1919—1921, vid norrlandskusten 1920—1923 med 1921 som toppåret. Sillfisket längs sydkusten upplevde en topp åren 1921—1922 och strömmingsfisket vid Västernorrlands kust en topp 1923. Fångsten av torsk ökade kraftigt i södra Östersjön åren 1919—1921 (HESSLE 1923).

1924 drunknade något hundratal tumlare vid Bornholm (JOHANSEN 1929). Vintern 1925 var rekordmild och bör ha gett en rik smoltklass. Sommaren 1925 var ett »smålaxår» vid norrlandskusten (OLOFSSON 1926). Smoltklassen

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[1] Det har sagts att tumlaren främst äter relativt små fiskar och att dess skadegörelse därför är begränsad. Detta torde vara en felsyn. Om den tar små fiskar, dock sådana som ej har andra naturliga fiender, blir tumlarens betydelse för fisket tvärtom större.

av 1925 gav en topp i Blekingefisket efter lax åren 1926—1928, vid Gotland 1927 och i övre Norrlands laxfiske åren 1927—1928.

1929 inträffade åter en tumlardöd genom drunkning i Bornholmsområdet (JOHANSEN 1929). Våren 1930 var mycket varm, liksom hela vintern varit. En rik smoltklass skapades åter och redan på sensommaren märktes en påfallande rikedom av smålaxar i Östersjön (ALM 1931), i december 1930 var antalet smålax utanför tyska kusten betydande (WILLER och QUEDNAU 1934) och sommaren 1931 var åter ett »smålaxår» längs norrlandskusten (OLOFSSON 1932). Blekingefisket efter lax fick en topp 1931—1932, fisket vid Gotland 1933 och i övre Norrland åren 1934—1935.

1940 drunknade många tumlare — möjligen i tusental — i Östersjön (ALANDER 1940, LÖNNBERG 1940). Dessutom fångades omkring 700 tumlare vid Gamborg åren 1941—1944 (MØHL-HANSEN 1954, LINDROTH 1957). Hos LINDROTH (1950) återfinns en missvisande uppgift om vintern 1942—1943 som kan ge intryck av att tumlare drunknat även denna vinter. Detta är ganska säkert felaktigt, vintern var ytterligt mild, liksom även den följande.

Vårarna 1940—1942 var kalla och har säkerligen gett dåliga smoltklasser. Däremot kunde vårarna 1943 och 1944 ge mycket goda smoltklasser, som därmed för första gången på allvar kunde utnyttja den reduktion tumlarna råkat ut för. Vi fick också en omedelbar och enastående stark effekt, med toppåren 1945—1947 inom hela Östersjöbäckenet. Ökningen började vid norrlandskusten bli märkbar redan 1941, men i större skala först med 1943 års smoltklass, som började återvända 1944. Förhållandena i Vänern var uppenbarligen likartade, bortsett från att primärfaktorn saknades, och vi fick en reaktion — endast i sekundärfluktuationen alltså — för Klarälvslaxen åren 1945—1947, precis samma år som ute i Östersjön.

Sillfisket vid sydkusten upplevde en ny högkonjunktur 1941—1945, vid östkusten 1942—1944. I stora delar av Östersjön var det under samma år så mycket torsk att magra »lustorskar» blev riksbekanta fenomen.

1947 inträffade en mindre tumlardöd vid Aerö (LINDROTH 1957). Våren 1948 var relativt kall, men våren 1949 varm och gav troligen en rik smoltklass. År 1952 åstadkom så denna smoltklass en viss tillfällig återhämtning i den annars fallande trenden i laxfisket. Eftersom även Klarälvens lax reagerade 1952 är dock toppen troligen främst beroende av sekundärfluktuationen.

7. Historik över tumlarhypotesen

Man torde kunna räkna med att frågan om tumlaren och laxen kommer att ådraga sig betydande uppmärksamhet i framtiden. Redan detta kan därför vara anledning att ge en återblick på hur denna hypotes uppkommit och dess korta historia hittills.

Fiskeritjänstemannen J. A. LING är den förste som haft ögonen öppna för tumlarens betydelse. Efter att i korthet 1901 ha omnämnt tumlaren som en av flera möjligheter till förklaring av det alltmer avtagande laxfisket, återkommer LING till ämnet i februari 1914, då han vänder sig till Svenska Fiskareförbundet med anhållan att vid föreningens instundande årsmöte den 20 mars samma år en diskussion anordnas angående vilken metod som bäst lämpade sig för fångst av tumlare. Han skriver:

»Det är kanske ej så allmänt kändt, men dock ett faktum, att tumlarnas antal i Bottenhafvet hastigt ökats under senare tid. Numera händer det ej sällan, att man vid kusten av Västernorrlands län samtidigt observerar rätt många af dessa skadedjur, ja ända till 7 à 8 st. De tränga ofta in i skärgården och uppehålla sig där äfven långt fram på hösten. För 30 år sedan var tumlaren mycket sällsynt i dessa trakter, och enstaka exemplar observerades endast med flera års mellanrum. En bidragande orsak till att de nu trifvas så bra är måhända den omständigheten, att *hafvet här utanför numera sällan tillfryser i den utsträckning, som förr anses ha varit fallet* (SVÄRDSON kurs).

Då den skada, som tumlarne vålla fisket, gifvetvis blifver allt större, ju mera djurens antal ökas, och då det är lättare att hämma ökningen nu än längre fram i tiden, har undertecknad för att väcka intresse för fångsten föreslagit att länets Hushållningssällskap måtte utbetala en premie af tio kronor för hvarje infångad tumlare. Om detta förslag bifalles, kommer frågan om bästa sättet för tumlarnes infångande att blifva mera aktuell än hittills, och har jag därföre tillåtit mig att på detta sätt framlägga frågan för Svenska Fiskareförbundet under förhoppning, att bland dess medlemmar någon eller några skulle vilja gifva anvisning om bästa fångstsättet.

Gifvet är att man här vid vår bergiga och branta kust ej kan tillämpa samma fångstmetoder som t.ex. i Danmark. Möjligen kan tumlaren fångas i särskilda härför afpassade *nät,* som utsättas i plogform i de sund, där djuren pläga stryka fram, men så länge ej några försök gjorts i denna riktning, kan metoden ej rekommenderas.»

Frågan togs mycket riktigt upp till debatt som LING önskat och i protokollet från sammanträdet heter det:

»Sedan *professor Lönnberg* beskrifvit de nu upphörda danska tumlarefångsterna i Lilla Bält, *byråchefen Nordqvist* påpekat att den skada tumlarna göra är vida mindre än den som skälarna åstadkomma, samt att numera särskilda redskap för tumlarefångst nog ej funnes, lämnades af *fiskeriassistenten Arwidsson* och *fiskeriinstruktör Eriksson* några meddelanden, gående ut på att någon större skadegörelse ej påbördades tumlarna. *Fiskeristipendiaten Nilsson,* omtalade, huru på Dalmatiens kuster tumlare, eller om det möjligen vore andra smärre tandhvalar, instängdes med nät och harpunerades. *Fiskeriassistenten Arwidsson* uppvisade ett tumlarenät, som han lyckats anskaffa från Albo härad i Skåne. Om användningssättet hade han ej fått närmare kännedom, men ännu torde personer lefva i den trakten, hvilka kunde lämna upplysningar härom. Frågan befanns vara för litet utredd, för att några beslut skulle kunna fattas» (Sv. Fiskeritidskrift 23: 40—41, 59—60).

Den protokollförda diskussionen är intressant eftersom den så tydligt visar hur kallsinnig den tidens samlade expertis ställde sig till tanken att tumlaren gjorde någon skada för fisket. Visserligen torde man väl med »skada» mest ha tänkt på redskapen, och att sälen söker ta fiskar som fastnar på nät kan väl betraktas som ett indicium på att den inte så lätt kan fånga en fisk i fria vattnet. Men att man inte bara räknade med skadegörelse på redskapen framgår av att man vid ungefär samma tid uttalat sig mycket fördömande om storskraken. Skrakarna och sälarna ansågs alltså på den tiden vara mycket skadliga för fisket medan tumlaren var ofarlig. Det är intressant att samma uppfattning fortfarande är vida spridd.

Det skulle dröja till slutet av 1940-talet innan tumlarhypotesen vaknade ur den dvala den hamnat i efter mötet i mars 1914. Den sensationella ökningen i laxbeståndet hade då kulminerat och det började alltmer stå klart att fenomenet sannolikt hade med fiskeförhållandena under kriget eller med de stränga vintrarna att göra. På Sötvattenslaboratoriet diskuterades frågan ganska ofta mellan ALM, HULT, LINDROTH och SVÄRDSON.

Fil. dr. HARALD ALANDER hade våren 1940 bevittnat de många döda tumlarna längs Skånes östra kust. Han skrev också en notis därom (ALANDER 1940). Vid ett besök på Sötvattenslaboratoriet, sannolikt 1948, råkade ALANDER bli indragen i en diskussion om laxfrågan. Det gällde närmast vilken laxfiende som kunde ha blivit så reducerad av de tre stränga vintrarna att laxökningen därmed kunde få en biologisk förklaring. Själv hade jag föreslagit gäddan som möjligen ansvarig, men även säl och skrak omnämndes. ALANDER föreslog då tumlaren och hänvisade till sina egna upplevelser från 1940 och till det faktum att arten efter detta föga synts till i Östersjön.

När LINDROTH (1950) gjorde sin sammanställning av det föreliggande materialet till belysning av laxbeståndets fluktuationer, kunde han även påvisa en suggestiv överensstämmelse mellan stränga vintrar och hög laxfångst. Tyvärr var en korrelation dock icke statistiskt säkerställd, men trolig. LINDROTH redovisade hypoteserna om gäddan, sälarna och tumlaren och hänvisade beträffande den sistnämnde till ALANDERS uppgift. Sambandet mellan stränga vintrar och hög laxfångst kunde alltså tänkas verka via laxfienderna, antingen i hav eller älv.

I sin sammanfattning formulerar LINDROTH själv sina slutresultat på följande sätt:

»Försöken att bland de tänkbara faktorerna gallra hårt ha inte gjorts alltför allvarliga; dels är det enligt min mening förkastligt och utsiktslöst att med nuvarande ofullständiga kunskaper söka utvälja någon viss såsom ansvarig för laxfångsternas fluktuationer, dels kunna inga av de i regel diskuterade faktorerna förklara de långperiodiga svängningarna. Och det är framför allt dessa framställningen gällt.

Jag har den uppfattningen, att fluktuationer i *av klimatfaktorer beroende biologiska jämviktsförhållanden äro den väsentliga orsaken till laxfångstens och laxbeståndens långsiktiga fluktuationer* så som de framträda i den utjämnade laxkurvan.»

Några år senare fick jag av en händelse JURVAS (1952) arbete om Östersjöns isläggning i mina händer. Jag insåg genast att här öppnade sig en ny möjlighet att mer ingående prova sambandet mellan istäckets utsträckning och laxfångsten. Eftersom jag dessutom sedan länge varit av den uppfattningen att det viktigaste inom laxforskningen var att utreda varför populationsökningen i mitten av 1940-talet inträffat, (uppfattningen offentligt framförd t.ex. 20 jan. 1948) påbörjade jag själv en sådan analys.

Därvid befanns (SVÄRDSON 1955), dels att de smärre fluktuationerna i laxfisket berodde på en klimatbunden inverkan på smoltklassernas och lekklassernas storlek, dels att den primära fluktuationen med största sannolikhet berodde på inverkan från tumlaren, medan övriga dittills aktuella laxfiender vid närmare granskning icke kunde antas ha så stor effekt på laxbeståndet.

Denna min artikel ådrog sig LINDROTHS kritik och därmed är vi framme vid denna artikel, där tumlarfrågan, liksom sekundärfluktuationen, förts ytterligare ett stycke framåt.

8. Praktiska konsekvenser och förslag

För att praktiskt prova hypotesen om tumlarens stora betydelse för laxbeståndet i Östersjön föreslag jag (SVÄRDSON 1955) en snarast, på försök, återupptagen tumlarfångst i Gamborg fjord, dvs den plats där de traditionellt fångats sedan medeltiden.

Till detta kan kanske läggas att, som framgått av redogörelsen på sid. 373—374 i flera fall tumlardöd lett till ökning i laxfångsten samt vidare att de två kraftigaste reduktionerna, där drunkning och mänsklig fångst sammanfallit, dvs åren 1916—1919 samt igen 1940—1944 lett till en ökning inte bara av laxbeståndet. Samtidigt har både sill- och torskfisket upplevt en markerad blomstring.

Är det nu ens möjligt att allt detta beror på hydrografiska förhållanden i havet? Och har vi verkligen moralisk rätt och ekonomisk råd att — med ansvaret inför det praktiska fiske vars förbättring den fiskeribiologiska forskningen har till huvuduppgift — följa LINDROTHS (1957) rekommendation:

»Enligt min mening får man icke utgå ifrån någon väsentlig inverkan av jakt på tumlarbeståndet och ett sannolikt mycket kostsamt försök att genom återupptagen jakt reducera tumlaren, såsom SVÄRDSON föreslår, bör föregås av undersökningar över tumlaren i Östersjö-området, samt tumlarens relation till laxen.»

Detta förslag är direkt opraktiskt. Ingen vet hur tumlare skall fångas i öppet hav, med vid Middelfart finns en tradition att bygga på. De undersökningar LINDROTH antyder erfordrar speciellt utbildad personal, medan fångsten vid Middelfart kan utföras av den lokala befolkningen. En stor mängd undersökta tumlare i Östersjön, som alla till äventyrs icke hade ätit lax, skulle i huvudfrågan icke bevisa något alls. Tumlarens predation på laxen kan vara både mycket lokal och ytterst kortvarig, men ändå betydelsefull. Och slutligen: *om de två gånger inträdande topparna av sill- och torskfisket beror på samma orsak som laxfiskets uppgång,* vad medför då LINDROTHs förslag för konsekvenser?

För tydlighetens skull vill jag tillägga att jag självfallet gärna ser att tumlarens dietvanor närmare utforskas, både i Östersjön och på andra håll, men det *mest praktiska* måste vara att snarast, på försök, återuppta fångsten vid Gamborg.

Personligen är det mig mycket motbjudande att föreslå ökad förföljelse av ett djur, som på grund av sina naturliga vanor klassificeras som skadedjur. Beträffande tumlaren är det dock i första hand fråga om ett praktiskt prov av en vetenskaplig hypotes. Det kan finnas möjligheter att påverka laxbeståndet inom Östersjöbäckenet i positiv riktning. Laxen har för närvarande en viktig plats i de diskussioner som förs mellan representanter för naturskyddssträvandena och kraftverksindustrins intressen.

Bergeforsens kraftverk blev ej tillåtet vid vattendomstolens behandling av ärendet och först genom Kungl. Maj:ts beslut beviljades tillstånd till uppförandet. Av de motstående intressen, som ansågs lida stor skada av det planerade bygget, var Indalsälvens laxfiske ett av de största. Laxen är en av de ytterligt få argument som naturskyddets representanter kan omvandla i pengar och därmed få vattendomstolarna att ta hänsyn till.

Den paradoxala situationen har därför inträtt att redan ur extremt naturvårdande synpunkter ett försök att höja laxbeståndets numerär måste framstå som synnerligen angeläget. Om det vore möjligt att genom kontinuerlig tumlarkontroll hålla laxbeståndet permanent uppe vid 1940-talets högsta nivå — personligen tror jag det är möjligt — skulle detta få de mest vittgående konsekvenser bl.a. för hela den aktuella avvägningsfrågan i samband med vattenkraftens utbyggnad.

De ekonomiska vinsterna av en genomförd kontroll, som gav positivt resultat kan icke tillnärmelsevis bedömas. Men så mycket kan sägas att om tumlaren har effekt inte bara på lax utan även på sill och torsk, vinsterna når mycket höga värden. De tre fiskarterna är ju de viktigaste inom Östersjön och av största betydelse för ett flertal länders fiskare.

Mest realistiskt och praktiskt i nuvarande läge torde vara att svenska och danska staten vardera tillskjuter så stora belopp att man för en provperiod kan utlova fångstmännen en premie på 100 kronor för varje tumlare. Dessutom bör fångstmannen givetvis ha full rätt att genom försäljning av tran etc. få ytterligare kompensation och ersättning för det arbete och den kostnad han nedlägger på fångst och redskap.

Att danska staten bör vara medintresserad är uppenbart. Samarbete om tumlaren skulle kanske lättare kunna ordnas än i fråga om minimimåttsbestämmelser. I det senare fallet har ena parten större nytta av samarbetet, medan detta, när det gäller tumlaren, alldeles uppenbart är fråga om ett ömsesidigt intresse.

9. Slutord

Med anledning av att kritik framförts mot ett tidigare arbete av författaren (SVÄRDSON 1955) har i denna nya artikel frågan om laxfiskets fluktuationer ånyo upptagits till granskning.

De i min tidigare artikel framförda resultaten att laxfiskets smärre fluktuationer bestämdes av växlingen mellan rika och fattiga smolt- och lekklasser har därvid framstått i ännu tydligare ljus. Den framförda kritiken har i stort sett helt kunnat avvisas såsom byggande på missförstånd och misstag medan den i några fall medfört en omformulering av det väsentliga i tidigare framförda synpunkter.

Beträffande primärfluktuationen har diskussionen ökat den redan förut stora indiciebördan mot tumlaren, såsom ansvarig för laxbeståndets stora växlingar.

Praktiska förslag ges och motiveras. De utmynnar i att svenska och danska staten genom premier bör stimulera till en intensiv försöksfångst av tumlare vid Gamborg fjord i Lilla Bält, Danmark.

10. Litteratur

ALANDER, H. 1940. Massdöd bland tumlarna i södra Östersjön. *Svensk Fiskeritidskrift 49: 207—208.*

ALM, G. 1924. Laxen och laxfiskets växlingar i Mörrumsån och andra Östersjöälvar. *Medd. Kungl. Lantbruksstyrelsen 252: 1—136.*

— 1931. Laxens egendomliga vandringar. *Svensk Fiskeritidskrift 40: 61—62.*

— 1934. Salmon in the baltic precincts. *Rapp. Procès-Verbaux Cons. Perm. L'explor. Mer. XCII: 1—64.*

BEHRENDT, CHR. 1929. Om Marsvinsjæger-Lauget i Middelfart. *Turistforeningen for Danmark, Aarbog 1929: 235—252.*

CARLIN, B. 1955. Försök med märkning av odlade laxungar. *Sv. vattenkraftföreningens publ. 451: 85—104.*

ERRINGTON, P. 1956. Factors limiting higher vertebrate populations. *Science 124: 304—307.*

FOERSTER, R. E. 1954. On the relation of adult sockeye salmon (*Oncorhynchus nerka*) returns to known smolt seaward migrations. *J. Fish. Res. Bd. Canada 11 (4): 339—350.*

HESSLE, CHR. 1923. Undersökningar rörande torsken (*Gadus callarias,* L.) i mellersta Östersjön och Bottenhavet. *Medd. Kungl. Lantbruksstyrelsen 243: 19—74.*

JACOBSEN, J. P. and A. C. JOHANSEN, 1921. On the causes of the fluctuations in the yield of some of our fisheries. 1. The salmon and sea trout fisheries. *Medd. Komm. Havundersøgelser VI (5): 1—48.*

JÄRVI, T. H. 1948. On the periodicity of salmon reproduction in the northern Baltic area and its causes. *Rapp. Procès-Verbaux. Cons. Perm. Int. L'explor. Mer. CXIX: 1—131.*

— and J. M. MENZIES, 1936. The interpretation of the zones on scales of salmon, sea trout and brown trout. *Rapp. Procès-Verbaux. Cons. Perm. Int. L'explor. Mer. XCVII: 1—63.*

JOHANSEN, A. C. 1929. Om Dødeligheden blandt Marsvin, Fisk og større Krebsdyr i Farvandene omkring Danmark under strenge Vintre. *Beretning Dansk. Biol. Station XXXV: 59—91.*

JURVA, R. 1952. On the variations and changes of freezing in the Baltic during the last 120 years. *Fennia 75: 17—24.*

LINDROTH, A. 1950. Laxbeståndets fluktuationer i de norrländska älvarna. *Sv. Vattenkraftföreningens publ. 415: 97—224.*

— 1955 a. Mergansers as salmon and trout predators in the River Indalsälven. *Rept. Inst. Freshwater Research, Drottningholm 36: 126—132.*

— 1955 b. Skraken som laxfiende. *Svensk Fiskeritidskrift 64: 121—122.*

— 1957. Baltic salmon fluctuations: a reply. *Rept. Inst. Freshwater Research, Drottningholm, 38: 109—130.*

LÖNNBERG, E. 1940. Massdöd av tumlare, *Phocaena communis. Fauna och Flora 35: 284.*

MØHL-HANSEN, U. 1954. Investigations on reproduction and growth of the porpoise (*Phocaena phocaena*) from the Baltic. *Vidensk. Medd. Dansk. naturh. Foren. 116:* 369—396.

NORDQVIST, O. 1906. Laxens uppstigande i Finlands och norra Sveriges elfvar. *Fennia 22 (2): 1—58.*

OLOFSSON, O. 1926. Några anteckningar om laxfisket i Norrbottens och Västerbottens län år 1925. *Svensk Fiskeritidskrift 35: 68—80.*

— 1932. 1931, ett nytt smålaxår i övre Norrland. *Svensk Fiskeritidskrift 41: 125—130.*

SCHEVILL, W. E. and BARBARA LAWRENCE, 1956. Food-finding by a captive porpoise (*Tursiops truncatus*). *Breviora Mus. Com. Zool. Cambr. Mass. 53: 1—15.*

SVÄRDSON, G. 1951. The Coregonid Problem. III. Whitefish from the Baltic, succesfully introduced into fresh waters in the north of Sweden. *Rept. Inst. Freshwater Research, Drottningholm 32: 79—125.*

— 1955. Salmon Stock Fluctuations in the Baltic Sea. *Rept. Inst. Freshwater Research, Drottningholm 36: 226—262.*

— 1956 a. Samspelet mellan lek- och utvandringsmognad. *Svensk Fiskeritidskrift 65: 4—10.*

— 1956 b. Populationsdynamik. *Statens Naturvetenskapliga Forskningsråds Årsbok 1955: 203—208.*

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

WILLER, A. und W. QUEDNAU. 1931. XI. Untersuchungen über den Lachs (*Salmo salar* L.). *Zeitschrift f. Fischerei 29: 185—215.*

11. Summary: The salmon and the climate

Introduction

My paper on the salmon stock fluctuations (1955) has been criticized by LINDROTH (1957) and this second paper on the subject is a shorter summary of my main viewpoints and a discussion of LINDROTH's paper.

Since my first article was written in English, as was LINDROTH's as well, the Swedish language in the larger part of my reply may seem surprising. Foreign readers may, therefore, be unable to follow the discussion in detail.

My second paper, however, may be easier available to those fishery administrators and organizations for fishermen, who are the persons most concerned with the practical aspects of this discussion. Apart from the theoretical interest in the population fluctuations of the salmon, great economic values are involved for all those engaged in the exploitation of the Baltic salmon stock.

The hypothesis presented in my 1955 paper can be tested in an experiment. Porpoise and salmon seem to be involved in a predator-prey relationship within the Baltic Sea and artificially or naturally raised porpoise mortality through hunting or severe ice conditions has repeatedly been followed by a rise in the salmon population.

The natural conditions within the Baltic Sea are extremely favourable for an experiment on porpoise control, since the whales annually move out through the Danish sounds where they were formerly hunted commercially. If this hunting should again be intensively practiced for only one or two winter seasons, we should probably know much more about the factors regulating the salmon stock.

Of course, it is now difficult to arouse the enthusiasm of the fishery administrators in Sweden and Denmark for this project, as LINDROTH has suggested more general scientific research on the porpoise as being more needed at the moment. This paper is, therefore, mainly written in Swedish, to make the arguments available to the fishermen and fishery administrators.

The short-term fluctuation

A hitherto unknown short-term population fluctuation of the Baltic salmon was described in my earlier paper (1955). It was correlated to climate in such a manner that peaks in the salmon catch of the rivers occurred 2—3 years after mild winters and again 4—6 years after severe winters. This short-term fluctuation is not accepted by LINDROTH. He thinks it is an artifact due to misinterpretation of statistical data on my part. Consequently, he also rejects the interpretation of its causes as suggested by me.

In the present paper the short-term fluctuation is confirmed by new statistical material from Gäddvik in the Lule River (Table 1). It can also be traced in the scanty material from Norrfors in the Ume River (Table 2). LINDROTH himself has made its existence more evident in my own material, from Svartö in the Lule River, by separating the catch data in two periods of high and low average yields. In the high-catch period the short-term fluctuation is extremely clear, but in the low-catch period it is less evident.

The last fact is the starting point for LINDROTH to argue that the short-term fluctuation is nonexistent or only an artifact, created by the long-term fluctuation which is also dependent on climate. The short-term fluctuation is, however, also evident in the Gäddvik material, coming from the low-catch period. Thus it is proved to exist in the Lule River for both periods.

In the opinion of the present writer, it cannot be seriously doubted that the short-term fluctuation is real. In the absence of detailed statistics from other rivers it has not so far been proved to exist in them, but it must be of a general nature as it gives the best explanation available for the fact that the long-term fluctuation (in all rivers) gives the very best correlation coefficient (0.42, P less than 0.001) for a lapse of 5—6 years between a winter of heavy ice cover and the salmon catch in the rivers. LINDROTH (his Table 2) has himself given proof that the correlation culminates with a lapse of these 5—6 years. This is due to the interaction between the short-term and the long-term fluctuation as described in the next chapter.

The interpretation of the biological nature of this short-term fluctuation was suggested by me as being temperature sensitivity of the hormonal transition phases of salmon, i.e. the smoltification and maturation. The maturation process was thought to be stimulated by high temperature in the sea and a great number of recorded facts laid down in the salmon literature were cited as evidence in favour of this hypothesis. The variation of salmon smolt age in different geographical areas, different rivers and the puzzling fact of trout smoltification and sex-ratio as well as the late emigration of large eels from northern Scandinavia were found to indicate a similar temperature sensitivity of the hormonal process, accompanying the »silvering» of migratory fish.

The editing of my first paper was rather difficult owing to the great number of recorded data that were included in support of the hypotheses. It is admitted that it could have been easier to read.

A number of models had been prepared but were not included in the paper, owing to the general uncertainty of the scale-readings performed on Baltic salmon. Salmon of known age were sampled and their age, as read on the scales, was not always coincident with the known age. Above all, the uncertainty was concentrated on the start of the pelagic sea-life (checks reported by JÄRVI and others) and again as to its termination. The reasons for this uncertainty regarding scale-readings were given.

LINDROTH thinks my interpretation is impossible. I can only admit that it might be still better. The shorter time available for predators if growth is accelerated during the very first period of life in the sea (FOERSTER 1954, SVÄRDSON 1955 p. 250) should be given more emphasis. Recent and unpublished research at this Institute has produced strong evidence that warm springs give better growth and higher survival in a number of freshwater fish species.

Thus an ultimate factor is at work, which may be responsible for the evolution of a proximate factor, acting through temperature stimulus in the river. If the survival of the smolts at the river mouth should be low in the cold sea after severe ice winters, then every reaction which delays the smoltification to next spring will be favoured by selection. In this way, the reaction to temperature stimuli during a short sensitive period will be easier to understand. The warm spring in the sea after a mild winter thus gives a high survival of those smolts descending, but also probably stimulates, through parallel temperature development in the river or through some other climatic factor usually accompanying a warm sea, accelerated smoltification of those parr which are "ripe".

Thus the short-term fluctuation is probably real and some interrelated hypotheses, which are by no means very advanced and bold but based on established experience, may give a satisfying biological interpretation.

The long-term fluctuation

This fluctuation has been known for a very long time. It was suggested as being correlated to ice conditions in the Baltic by LINDROTH (1950) and this was later proved statistically by SVÄRDSON (1955), with some new data on the ice cover of the Baltic.

Several predators, sensitive to severe winters, were outlined as causative by LINDROTH, i.e. porpoise and seals. Later (1955) he found mergansers prey on salmon in the Indalsälven River to such an extent that they could be an active agent behind the correlation found.

In my earlier paper, (SVÄRDSON 1955), evidence was produced that porpoise was the probable sole predator causing the known fluctuations of the salmon stock according to the ice cover of the Baltic. It was further found that the artificial mortality of the porpoise, created by man when hunting them in the Danish sounds, was probably of such magnitude as to give a rise in the salmon stock.

Two objections against the porpoise as the main factor have been raised. They are again discussed by LINDROTH in his critical paper. First, the landlocked salmon of Lake Vänern has shown some tendency to fluctuate parallel to that of the other rivers, mainly by having a peak in 1945—1947. Secondly, the spectacular rise of the Baltic salmon stock during the 1940's culminated in 1945—1947, while the known great porpoise mortality from the ice was recognized as having occurred in 1940.

Both objections fail when the interaction between the short-term and the long-term fluctuation is considered. In the short-term fluctuation a bad smolt-class and a low survival of smolts during the very first weeks in the sea accompanies a cold spring. A severe ice-covering in the Baltic may kill a great number of porpoises and thus give rise to salmon abundance. But, owing to the cold spring that follows a severe winter, the first smolt generation, which should profit by the porpoise reduction, is also reduced in number. They give a deficit to the river catch during the next four years. But the second smolt generation, produced after the porpoise kill, will fully benefit from the situation and give a peak in the river catch after a lapse of 4—6 years. The warmer this second spring is, the higher the peak will be.

Now, in Lake Vänern only the short-term fluctuation was at work in the 1940's. The springs of the years 1940—1942 were extremely cold and smolt production and survival must have been very low. Not until 1943, and again 1944, were the springs mild and production and survival of smolts probably high. Thus a (low!) peak in the river catch of returning salmon should come in 1945—1947.

In the Baltic Sea, the smolt generations were relatively of the same magnitude. But, owing to the porpoise kill in 1940, the survival of the 1943 generation of smolts was quite extra-ordinary and gave the record peak yield in 1946. A general increase, however, was noticed from 1941 onwards, and though 1946 was the peak year, the catch was high until the beginning of the 1950's. The catch has fallen steadily since then.

My splitting of the fluctuations of the salmon stock into two waves of population fluctuation differing in principle (SVÄRDSON 1955), has thus enabled a more thorough analysis of its nature. Both are dependent on climate, both are probably due to the action of predators, but the differences between them are important to realize. Both may be tested by experiments. The short-term fluctuation will soon be automatically tested in the routine work of releasing marked smolt by Dr. CARLIN and the porpoise-factor will at least be naturally tested by severe winters sooner or later.

On the Growth Structure and Developmental Physiology of the Scale of Fishes

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An almost incalculable number of investigations into the scale of fishes has been carried out during the last 150 years. The great interest of the scientists can be explained mainly by two reasons. During the 19th century a classification of the multiform groups of fishes was a desideratum, and the morphological characters of the scales were thought to be of great value in this connection. Towards the end of the century the interest was deflected in another direction. Hoffbauer's papers provided the possibility of determining age and growth of fishes by means of the scales, and the ensuing investigations dealt partly with the histology of the scale and partly with the elaboration of the method for the determination of the age. There is no doubt that the greatest progress has been made along the second line. This has led to the peculiar situation that we possess practically applicable methods without having any deeper knowledge of the structures upon which these methods are based. For this reason continued investigations into the formation of the scales are necessary, particularly as the scientists carrying out research in the field find themselves more or less in a blind alley on account of the lacking support on the part of the representatives for the basic studies. "It is high time for the carrying out of profounder investigations into the morphology and the histology of growing scales of fishes and the surrounding tissues".[1] (N. I. Tschuganova, *Acad. NAUK, SSSR, 34/5, 1099, 1955*).

This investigation is based mainly upon the roach and its scales. This fish has been chosen partly because it is easily procurable, and partly because its scales are rich in striae, i.e. the formation of striae is an often occurring phenomenon. Since the origin of the striae has been one of the most important problems of the investigations, the scales of the roach therefore provided many opportunities for studies. In other respects, however, the choice of the roach as object for the experiments has been less advantageous. Its growth, for instance, is too slow for obtaining upon its scales a distinct growth reaction upon treatment with Stoeltzner's method. This reaction might possibly turn out more distinct upon material from smaller waters with a faster rise of temperature during spring and with a distinct period with cold water during the winter. The roach is also often the victim of ectoparasites as well

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[1] Author's translation.

as of endoparasites, circumstances which render experiments of greater duration in the aquarium rather difficult.

Unless a different statement is made scales and adjacent tissues have been fixed in absolute alcohol for the histological examination. Otherwise the most common fixation fluids, like BOUIN's formula and formalin, have been used, although only to a minor extent.

For the demonstration of the mineral component in the scale and for the staining of the boundaries of the cells mainly STOELTZNER's method (1905) has been employed. The object is treated first with a solution of a salt of cobalt, resulting in a combination of the ions of cobalt and the phosphate groups in the bone salts. On the subsequent transfer of the object into a solution of ammonium sulphide brown or black coloured sulphide of cobalt is formed. The distribution of this coloured compound will thus coincide with that of the bone salts.

The scale of the roach is formed in a scale papilla, i.e. in an agglomeration of cells forming several layers in the dermis. The scale consists of two layers, the osseous layer and the fibrillary plate. The former is homogenous with the exception of a thin limiting layer covering its surface. The surface of the osseous layer carries ridges, the striae, running more or less parallel with the edge of the scale. The outer slope of the stria, i.e. the one facing the periphery, is usually much less inclined than the slope directed towards the centre, the "focus" (see Fig. 1). The edges of the crests of the striae often carry teeth (Fig. 1). The furrow between two striae will in the following be called the trough.

The fibrillary plate is built up of a number of lamellae which in their turn consists of bundles of fibres. The fibres in the lamellae are arranged in such a way that the directions of the fibres in two adjacent lamellae include an angle of 60°—90°.

More Important Older Examinations of the Scales of Fishes

The origin of the first anlages of the scales in the young fish has been examined by a number of scientists (KLAATSCH 1890, HASE 1907, 1911, PAGET 1920, PEVSNER 1926, SETNA 1934, FACH 1936, NEAVE 1940, DIETRICH 1953, YAMADA and SAITO 1953). Most of them are agreed upon that the anlage of the scale is formed in a dermal scale papilla. Some of them also observe that the first papillae are formed in the neighbourhood of the lateral line in the anterior half of the fish; this applies to the perch (HASE 1911) and the goldfish (NEAVE 1940). KLAATSCH (1890), PAGET (1920) and YAMADA and SAITO (1953) on the other hand find that the formation of scales starts in the posterior part of the fish in the trout (*Salmo trutta fario* L.), the herring (*Clupea harengus* L.), and the rainbow trout (*Salmo irideus*

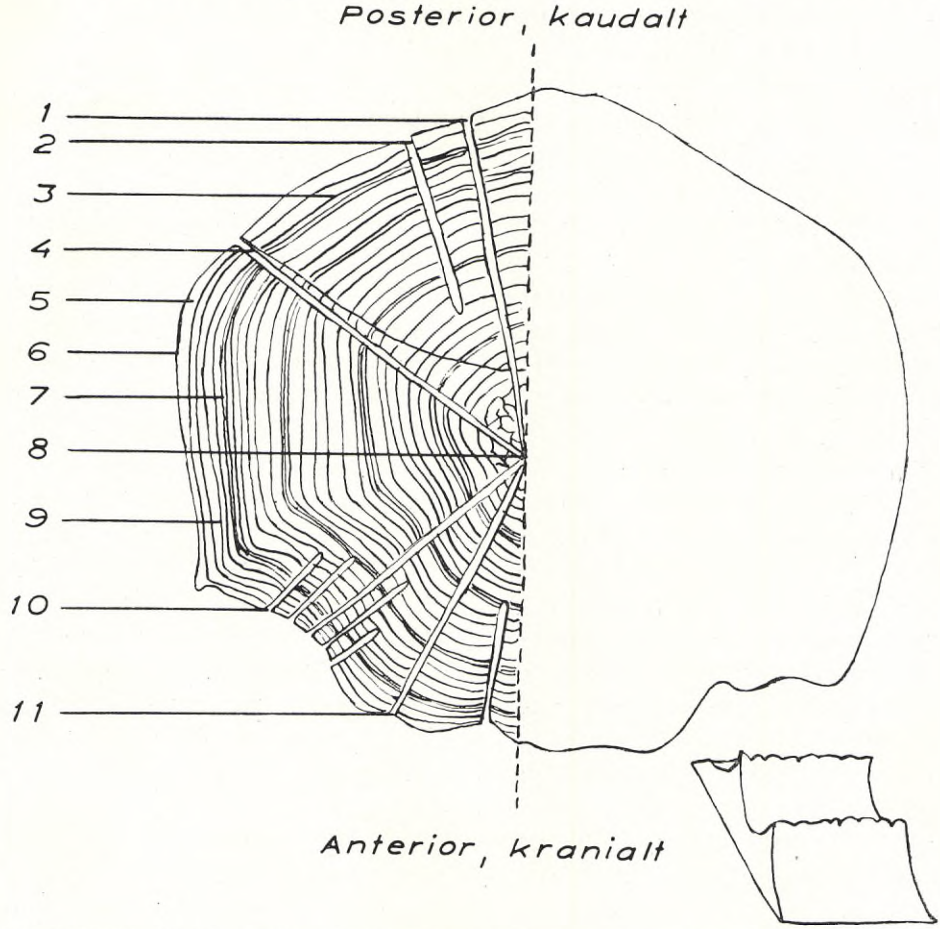


Fig. 1. Scale of roach, schematically. The right lower corner of the picture contains a sketch of the superficial sculpture of the striae with typical "teeth" upon their crests. 1 = complete radius from the exposed part of the scale; 2 = incomplete radius from the exposed part of the scale; 3 = exposed part of the scale; 4 = radius which together with the corresponding radius upon the other half of the scale and in connection with the myomeres forms "bending lines"; 5 = stria; 6 = "summer ring"; 7 = "winter ring"; 8 = focus; 9 = unexposed part of the scale; 10 = incomplete radius from the unexposed part of the scale; 11 = complete radius from the unexposed part of the scale.

GIBB.), respectively; from there it subsequently spreads in anterior direction and towards the back and the belly. NEAVE is of the opinion that the cells in the papillae which form the scales are not formed *in situ* by the tranformation of cells in the connective tissue. They should be differentiated from the mesenchym at the lateral line, and should migrate from this position to the place of the papilla under formation, where they arrange themselves in two layers.

Earlier authors have been interested mainly in the number of layers of cells and in their activity in connection with the formation of the scale, and also in the chronology of the development of the osseous layer and the fibrillary plate.

KLAATSCH (1890) describes two layers of "scleroblasts" on top of the osseous layer. At the margin of the scale these pass into a single layer. The plasm of the "scleroblasts" contains an unstainable spot. Its content is excreted, solidifies, and enters into the formation of the osseous layer. The striae are formed by the cells of the outer layer which arrange themselves at regular intervals parallel with the margin of the scale. The configuration of the striae is thus determined entirely by the arrangement of the cells.

The fibrillary plate is formed later than the osseous layer. It consists of connective tissue which is added unto the osseous layer from the bottom of the scale pocket.

NUSBAUM (1907) is of the opinion that the scale papilla consists of two layers of cells. Only the upper one, which peripherally consists of several layers, forms by secretion the osseous layer. The striae are the result of combined osteogenesis and osteolysis. Gradually the cells at the lower side of the osseous layer become arranged in two layers. The lamellae in the fibre plate are excreted from the interior of these layers.

Both PAGET (1920) and PEVSNER (1926) are of the opinion that the osseous layer represents the solidified secretion of the "scleroblasts". The striae are formed outside a ring of cells. According to PAGET osseous layer and fibrillary plate are formed about simultaneously. PEVSNER, on the other hand, declares herself capable to demonstrate that the fibrillary plate originates earlier than the osseous layer.

SETNA (1934) described four layers of cells. The secretion of the two upper layers gives rise to the osseous layer, the other two forming in the same way the fibrillary plate. The striae arise peripherally within agglomerations of cells.

When studying the scales of *Phoxinus* FACH (1936) strongly insists upon that the scale of the fishes is an ectodermal formation. He believes that the caudal, exposed part of the scale penetrates into the epidermis. Leydig's cells in the epidermis secrete "Kalkmilch" (lime-water) which solidifies upon the fibrous ground-mass of the scale. This transport of material might possibly take place at the caudal part of the scale, but it is difficult to imagine how the secretion could be transported to the scale pocket which is sunk deeply into the dermis. After having rejected the possibility of a rotation of the scale in the scale pocket Fach nevertheless considers himself able to point out special cells, lepidoblasts, which lead the material for the scale towards the latter. The striae are formed when the flowing calcareous mass solidifies in the conducts towards the scale.

Criticizing FACH's paper NEAVE (1940) points out amongst others that the distribution of Leydig's cells not in any way indicates a connection with the formation of the scales. Besides, the osseous layer is not calcified at the beginning of its formation.

NEAVE (1936, quoted from NEAVE 1940) examines the formation of the striae, and arrives at the same result as NUSBAUM. Thus the striae should be developed by a simultaneous building up and disintegration of the osseous layer. Later (1940) he abandons this hypothesis. He now believes the striae to be formed of the same cells as the rest of the osseous layer. They are conditioned by a surplus of scale-forming material in the intercellular fluid at the edge of the scale. This material is deposited in the neighbourhood, and causes local thickenings of the osseous layer, the striae. In young scales NEAVE identifies two layers of cells above the osseous layer, and one layer below the fibrillary plate. The active cells in the periphery of the scale he conceives as osteoblasts, the inactive cells above the surface of the scale as osteocytes. He finds the osseous layer to be formed prior to the fibre plate. The first lamella of the former is formed by osteoblasts which then disappear. The continued growth of the fibrillary plate is effected by the incorporation of fibres from the bottom of the scale pocket.

Also DIETRICH (1953) exhibits a great interest in the number of the layers of cells. On the whole she follows NEAVE's investigations. For the formation of the striae, however, she advances a new theory: It is possible that one layer of cells does not supply enough material, while two layers provide too much. She thus thinks that the lower layer forms the main mass of the osseous layer, while the upper layer forms striae in the places, where these latter are in contact with the cells.

A question of essential importance in the later parts of this paper, viz. the course of the calcification, has not at all or hardly been touched upon by the authors referred to above. It has been established that the osseous layer is more strongly calcified than the fibre plate (KLAATSCH). NEAVE find the osseous layer to be initially uncalcified. He shows that the periphery of the osseous layer is uncalcified even in older scales.

Literature contains only a small amount of information about the organic composition of the scale of fishes. KLAATSCH considers the fibre plate to be a kind of connective tissue, and thus collagenous. GREEN and TOWER (1901) report the composition as collagen (76 %) and ichthylepidin (24 %); the latter is an albuminoid, intermediate between collagen and keratin. With the help of histological methods PEVSNER demonstrates the occurrence in the fibrillary plate of elastin. Neave considers the osseous layer to be collagenous. A recently formed fibrillary plate he considers to consist of collagen, which is, however, gradually impregnated with ichthylepidin.

A large number of papers have on the whole elucidated the formation and the structure of the collagen. The origin and function of the cement matter surrounding the fibres is known in part. But several problems are still waiting to be solved in this connection. Since the scale of fishes can be considered as a kind of bone, it might be justified here to give a brief summary of the formation and the properties of the osseous matrix (the osseoid).

The collagen is of cellular origin both in non-calcified and in calcified connective tissue (bone). In the former case it is formed by fibroblasts, in the latter by osteoblasts. There is no great morphological difference between these cells, the osteoblasts being as a rule more compact and shorter than the fusiform fibroblasts. From the physiological point of view, however, the difference is considerable, as the property of depositing lime in the cement matter around the collagenous fibres ought to be ascribable to the osteoblasts. Both types of cells form fibrils which outside of the cells unite into fibres (PORTER 1951, WASSERMANN 1954, JACKSON 1954). On account of their high content of ribonucleic acid the cells are at the same time basophilous (FOLLIS 1951, PRITCHARD 1952). Alkaline phosphatase appears both intracellularly and in the newly formed fibres, but appears also in connection with the calcification. The mucopolysaccharides in the cement matter are probably formed by the cells. So far the only experimental support of this theory is found in the occurrence of the PAS-positive intracellular granules which have been demonstrated by HELLER-STEINBERG (1951).

Histochemical Identification of the Cells Forming the Scales

The arrangement of the cells around the scale

Introduction. As has been reported already the number of the layers of cells and their influence upon the formation of the scales have received different interpretations. Since the problem is still not finally solved an attempt must be made to determine by means of new methods which cells take an active part in the first formation of the scale.

Methods. As the thickness of the scales of fishes is small it falls, at least under lower magnifications, entirely within the depth of focus of the microscopical objective. This causes difficulties e.g. in the determination of the number and position of the layers of cells in the entire object. A simple stereoscopic attachment has therefore been produced in order to intensify the impression of three-dimensional depth.

The attachment consists of a polarizer and two analysers, one for each of the oculars. The polarizer is divided into two halves, their optical oscillation planes including an angle of 90°. The polarizer is fitted so that the joint in the middle coincides with the perpendicular line through the field of view. A rotation of the analysers then divides the field of view into two halves which are alternatively illuminated and darkened. If the two inner fields in the analysers are darkened at the same time, the pictures of an object in the two oculars will not exactly coincide, producing thereby a three-dimensional picture of the whole. (The attachment has been manufactured according to verbal instructions of Prof. A. Wilska, Helsingfors).

Results and discussion. The surface of the osseous layer is overlain by two layers of cells. Of the cells of the lower layer only an inconsiderable amount of the plasm is left. The nucleus lies as a rule in the deepest part of the trough, with its longitudinal axis in alignment with the stria. The boundaries of the cells follow, and cross, the trough, respectively. The upper epithelium-like layer consists of polygonal cells which rest against the crests of the striae, but the course of the boundaries of the cells is independent of the striae (cf. NEAVE 1940, Fig. 1).

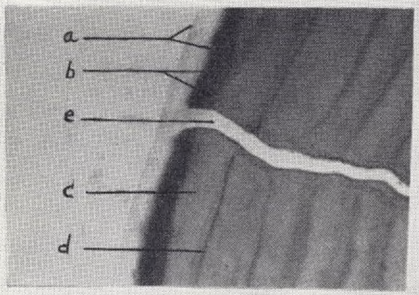
The osseous layer can be divided into three zones (Plate 1). Outermost we find a zone of uncalcified osseoid, followed by a zone of calcification and the entirely calcified part of the scale. The osseoid and the zone of calcification together form the zone of growth of the osseous layer. (This has so far not been defined more closely. Dietrich, e.g. speaks only of "the growing edge of the scale" without indicating any boundaries). Within it is formed the collagen matrix of the osseous layer which later calcifies (see below). After the termination of the calcification the osseous layer is not subject to any changes except perhaps resorbtion.

The zone of growth of the edge of the scale is surrounded on the upper side as well as on the lower side by an undetermined number of layers of cells. In an entire preparation the lower side of the scale is covered by *one* layer of cells. The statement by NEAVE about the direct connection between layers belonging to the upper and the lower side of the scale can not be verified as no boundaries can be distinguished between the layers in the zone of growth. In sections, particularly of regenerated scales, the bottom of the scale pocket can be seen to contain an additional layer which is in close contract with the cells forming the lamellae.

The extreme edge of the zone of growth is covered by some strands of thin elongated cells. Inside the edge the cells are shortened, the plasm is strongly basophilous, and the nucleus contains one or several large nucleoles. Especially at the regeneration of scales the strongly active cells, i.e. those which are about to produce extracellular material, are elongated, and show a polar arrangement with regard to the matrix (Plate 2). The nucleus is shifted to the part of the cell which is farthest from the scale. Often the part without nucleus merges directly into the matrix. In normally growing scales the cells are flatter, and have no or only feeble polarity.

Reactions of the cells to staining with methyl green-pyronine

Results and discussion. In sections untreated as well as decalcified with 5 % formic acid (*Lillie* 1951) and subsequently stained with methyl green--pyronine both the plasm of the cells and the nucleoles in the cells surrounding



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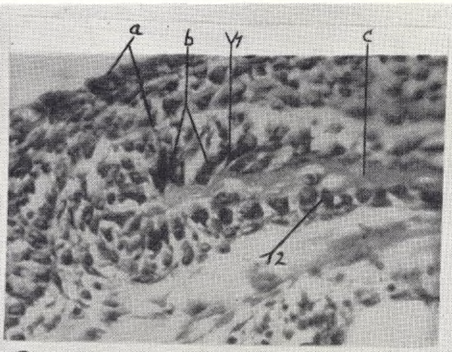

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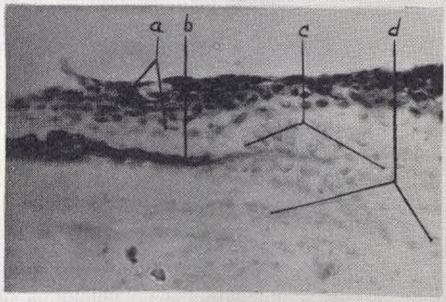

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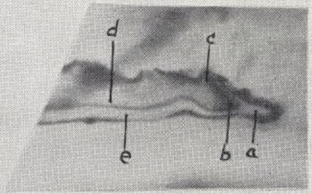

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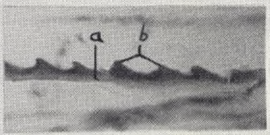

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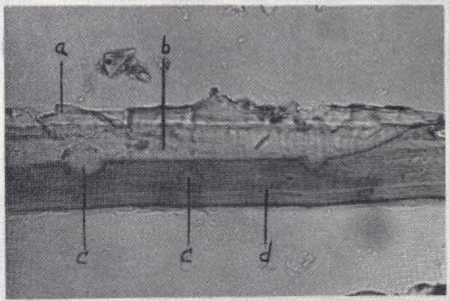

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Plate 1. Periphery of the scale of the fish. STOELTZNER's reaction, whole mount. a = osseoid zone, b = zone of calcification, c = completely calcified scale, d = stria, e = radius. × 500.

Plate 2. Section through the periphery of a regenerating scale. Methyl green-pyronine. a = epidermis, b = active scale-forming cells, c = scale. The arrows indicate: 1 the direct transition between cell and scale, 2 active cells upon the lower surface of the scale. × 980.

Plate 3. Periphery of a scale in regeneration. GOMORI's reaction on alkaline phosphatase. a = epidermis, b = scale, c = aktive scale-forming cells, d = cells in the dermis. × 700.

the zone of growth exhibit strong pyroninophilia. This reaction often points to a high content of ribonucleic acid (RNA). For the sake of control incubation was carried out in the specific enzyme ribonuclease (according to MC DONALD 1948) and in 10 % perchloric acid (GÖSSNER 1954). Both incubations removed the pyroninophilia. It can thus be considered proved that the pyroninophilia depends on the presence of ribonucleic acid.

It has been shown (CASPERSSON 1947) that a high content of RNA in nucleoles and cytoplasm always goes hand in hand with production of proteins. Thus osteoblasts (HELLER and others 1950, FOLLIS 1951, PRITCHARD 1952) and ameloblasts (BEVELANDER and JOHNSON 1945) have a high content of cytoplasm-RNA, when bone and enamel are being preformed. The combination of ribonucleic acid in the plasm and of intra- as well as of extranuclear alkaline phosphatase is typical for the formation of fibrous proteins (PRITCHARD 1956, BRADFIELD 1949, 1950).

It can thus be stated with the greatest probabitity that the cells surrounding the growth zone of the osseous layer upon the upper side as well as upon the lower side (with the exception of the outermost fusiform cells) form the collagen matrix which then calcifies. The two layers of cells on top of the osseous layer are formed only at the cessation of the activity. There is thus no foundation for DIETRICH's hypothesis that the uppermost layer should be the one which specifically forms the striae. In agreement with NEAVE the writer interprets these cells as a special type of osteoblasts which are not surrounded by bone tissue.

The occurrence of phosphatase activity and of glycogen in the formation of scales

Alkaline phosphatase

Introduction. The activity of phosphatase in lower vertebrates has previously been examined histochemically, e.g. by LORCH (1949 a, b) and DELSOL (1953), and with biochemical methods by BODANSKY and others (1931) and by ROCHE and others (1939, 1940). LORCH finds that alkaline phosphatase

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Plate 4. Section through the periphery of the scale. Toluidine blue. a = osseoid zone, b = zone of calcification, c = stria, d = calcified part of fibrillary plate, e = uncalcified lamella. Note the thin osseoid upon the outer slope of the stria and the direct transition between osseoid and fibre plate. × 1100.

Plate 5. Osseous layer of the scale. Decalcified, toluidine blue. a = osseous layer, b = striae. × 700.

Plate 6. Section through scale of roach. Toluidine blue. a = osseous layer, b = calcified part of fibrillary plate, c = Mandlian bodies, d = lamellae of collagen. × 750.

Plate 7. Mineral crystallites in the fibrillary plate at the edge of resorption. STOELTZNER. × 1550.

always occurs in young salmon at the formation of fibres and the ossification of bone. DELSOL proves the occurrence of alkaline phosphatase in the kidneys, the small intestine, and the epithelium of the gills in fishes. According to him the quantity of the enzyme in fishes is smaller than in the corresponding organs of higher animals. Teeth and scales contain a considerably greater amount of enzyme than other calcified tissues (ROCHE and others), but the amount of enzyme in the skeleton is smaller than that in kidney and small intestine (BODANSKY and others). In scales of *Clupea pilchardus* Walb. the amount of alkaline phosphatase is much greater during spring and summer, while the scale is growing, than during the remainder of the year (ROCHE, COLLET, and MORGUE 1940). Determinations of the activity of the enzyme in scales have been carried out on scales with the adjacent skin. The fact that the epidermis exhibits a strong enzyme activity (see below) must have formed a source of considerable inaccuracy in the above mentioned investigations. No histochemical examination of the activity of the alkaline phosphatase in scales prior to that presented here is known.

Methods. For proving the presence of alkaline phosphatase the following methods have been employed: the "revised method" of GOMORI, with and without decalcification (GLICK 1951), pH 6.8—9.6 (veronal buffer), modifications according to LORCH (1947) and SKJERVEN (1953). The time of incubation has varied between 1 minute and three days at temperatures between 18° and 37° C. In some cases adenylic acid prepared from yeast or muscles and sodiumdiphenylphosphate have been substituted for the Na-glycerophosphate as substrate for the enzyme.

Results and discussion. In no case, neither in connection with normal nor with regenerated scales, could alkaline phosphatase be demonstrated in connective tissue, active cells, or scale matrix.

Several reasons exclude the possibility that the negative reaction should be due to methodological faults. We thus find, in one and the same section, the epidermis to give a strong positive reaction in the case of regenerating scales of the roach, while scales which are growing rapidly are entirely negative (Plate 3). The reaction has also been carried out on cross-sections of young *Lebistes* from the nose to the terminal fin. Alkaline phosphatase is, amongst others, found in the retina, the epithelium of the olfactory pit, certain parts of brain and spinal marrow, the erythrocytes in the gills, the tubules of the kidney, and the small intestine. It is particularly interesting that dermal bones in the skull and the fin rays give a positive reaction, while the scales, both normal and regenerated, are negative.

RUYTER (1952) has found that large quantities of calcium phosphate, liberated from high concentrations of enzyme, suppress the reaction of cobaltous sulphide, and thus give negative results. For this reason very short times of incubation, 1—5 minutes, have been tried, also with negative result.

The majority of the histochemical investigations into alkaline phosphatase has been carried out on mammalian tissues. The temperature of incubation was kept at 37° C. As the body temperature of the fishes examined here never rises to this point, and as their enzyme might be inactivated at this temperature, temperatures of incubation down to 18° C have been tried.

The enzyme has its pH-optimum at 9.0—9.6. On regenerating scales of roach a series of experiments has been carried out with varying pH (6.8—9.6) and a difference of 0.2 pH-units between each couple of experiments. At pH between 9.0 and 9.4 the epidermis gives a positive reaction. The other tissues are negative.

The importance of the phosphatase for the formation of bone is still unknown. Two main theories have been advanced. 1) The enzyme liberates phosphate ions which, together with ions of calcium, are precipitated as calcium phospate. This theory was founded in the 1920's by ROBINSON and collaborators. Recently, however, NEUMAN and NEUMAN (1953) have shown that the crystal structure of the calcium phosphate cannot arise spontaneously by precipitation, but requires a gradual crystallization around a "nucleus of crystallization". Investigations, amongst others, by HOROWITZ (1942), GOMORI (1943), MOOG (1944), LORCH (1949 a), BEVELANDER and JOHNSON (1950), and PRITCHARD (1952) have, however, adduced strong arguments in favour of a close connection between the occurrence of alkaline phosphatase and calcification. Horowitz and Gomori, e.g., find that all cartilage which is to be ossified develops a positive reaction to phosphatase. Thus no calcification of cartilage should occur without the assistance of this enzyme, and calcification should start about 24 hours after the enzyme has attained maximal activity (MOOG). And in the *Elasmabranchia* only the cartilage which has shown extracellular phosphatase becomes calcified (LORCH). There exist, however, exceptions from this rule. Abnormal calcification of hyaline connective tissue in arteriosclerosis takes place without the collaboration of alkaline phosphatase (GOMORI 1943). The enzyme is missing also in the calcification of the epiphyseal cartilage of frogs and in the healing process of fractures of bones in these animals (PRITCHARD 1950).

2) The enzyme contributes to the formation of the bone matrix and the "ripening", i.e. the concentration of acid mucopolysaccharides in the cement matter. FELL and DANIELLI (1943) and DANIELLI and others (1943) have found the first-formed fibres in the healing of wounds to contain phosphatase, and BOURNE (1943 a, b) in addition the first fibres on the occasion of the regeneration of bones. MOOG and WENGER (1952) and KROON (1952) are of the opinion that the phosphatase hydrolyses glycose esters. The liberated glycose should then enter into the mucopolysaccharides of the matrix.

Glycogen

Results and discussion. It is an interesting fact that the cells forming the scales lack also glycogen. The methods according to HOTCHKISS (GLICK 1951) and BAUER-FEULGEN (GLICK 1951) for the establishment of its existence have been employed. In muscles grains of glycogen, which can be removed with saliva, have been demonstrated in the same section in which the scale-forming cells are negative. Errors of method seem therefore to be excluded. Polysaccharides have on the other hand been demonstrated in the osseous layer as well as in the fibrillary plate. (See furthermore pp. 398 ff.).

The only remaining possibility for the occurrence of phosphatase and glycogen in connection with the formation of the scales, in spite of the fact that their presence could not be demonstrated with the methods used, would be their occurrence in concentrations which lie below the threshold of sensibility of the reactions. Even in this case this small amount of alkaline phosphatase or glycogen, respectively, in the scale-forming cells would assign to these latter a special position among all fibre producing cells. The scale-forming cells can be compared most closely with osteoblasts in embryonic bone. These exhibit a high concentration of alkaline phosphatase, and in the pre-osteoblast stage contain glycogen.

The high concentration of glycogen in cells of connective tissue which are differentiated into embryonic osteoblasts, and its disappearance in connection with an increasing activity of the phosphatase have been considered to indicate that the presence of glycogen is a necessary condition for the formation of bone. PRITCHARD (1956) was, however, unable to demonstrate the occurrence of glycogen in osteoblasts which were differentiated in the healing of fractures. From the fact that glycogen is found in many types of cells in the embryonic stage, but not in the corresponding cells of the adult animal he draws the conclusion that the embryonic storage of glycogen might be an adaptation to the embryonic stage. In this case it would have nothing to do with the formation of bone as such.

At the present state of our knowledge about the formation of bone the absence of alkaline phosphatase at the formation and during the growth of the scale is unexplainable. Even if the phosphatase seems to lack importance for the process of calcification it seems, nevertheless, to be intimately linked up with the production of fibrillar proteins and with the differentiation of osteoblasts from the mesenchym. Since the collagen of the scale is a typical fibrillar protein, and since the differentiation of the scale-forming cells can be followed upon thin sections, the necessary conditions for the observation of the activity of the phosphatase, particularly during regeneration, are well fulfilled. Statements in earlier papers, especially by PRITCHARD, point, however, to — on the whole — lower concentrations of the enzymes in the lower vertebrates as compared with mammals (see above, p. 000).

If it is the task of the glycogen to lead to the formation of hexose esters which then form the substrate for the phosphatase it is natural that both the enzyme and the glycogen are missing at the same time. It is remarkable that the rest of the formation of the bone in *Lebistes* is accompanied by activity of phosphatase. The scales of the fishes obviously represent a special, simplified type of bone which is formed without the assistance of either alkaline phosphatase or glycogen. Earlier statements regarding a chemical isolation of the enzyme from scales are probably due to the occurrence of phosphatase in the epidermis (see above, p. 394), since these examinations were carried out on skin and not on scales.

The Calcification of the Osseous Layer

Introduction. It has already been mentioned that older investigations into the scales of fishes devoted only little interest to the process of calcification. NEAVE was the first to establish by means of v. KOSSA's method the occurrence of an osseoid zone in the extreme edge of the scales of the goldfish. The rest of the osseous layer is calcified.

During later times the composition of the mineral component and the chemistry of the process of calcification in bone has been studied with great intensity. According to general opinion the inorganic component is hydroxyapatite, $3\ Ca_3\ (PO_4)_2 \cdot Ca\ (OH)_2$, with adsorbed carbonate. The crystals are very small, about $500 \times 250 \times 100$ Å, giving a surface of bone of about 100—200 m^2/g (NEUMAN 1950). They are linked to the cement matter which surrounds the collagenous fibres. There seems to exist a connection between the period of the collagen of about 640 Å and at least those of the crystals which are in closest proximity to the fibres (BECHER and others 1954, FERNANDEZ-MORAN and ENGSTRÖM 1956). The cement matter contains chondroitin sulfuric acid which has been identified in most normal, calcified tissues, like dentine and enamel (PINCUS 1950, BEVELANDER and JOHNSON 1955), and in tendons (RUBIN and HOWARD 1950), but also in pathologically calcified arteries (FABER 1949). In connection with the calcification a strongly increasing amount of sulphate groups is embedded into the chondroitin sulfuric acid (DZIEWIATKOWSKY 1949, 1951). Metachromasy depending on free acid groups disappears with the calcification, but returns after decalcification (RUBIN and HOWARD 1950, PRITCHARD 1952). Protamine and methylene blue, which are bound to the chondroitin sulfuric acid, check calcification *in vitro,* the effect being in direct ratio to their concentrations (SOBEL 1952). Thus it appears probable at present that the calcification is initiated by a binding between Ca^{++} and the acid groups of the chondroitin sulfuric acid. Immediately afterwards the phosphate groups are bound, but in a higher concentration than in the hydroxyapatite. This is supported by the finding of ROCHE and MORGUE (1942) that the quotient Ca/P is low (0,38) at the beginning of the calcification, but rises gradually to 1,91—2,0, and thus closely approaches the theoretical value of 1,96.

Methods. In the course of the present investigation the calcification has been followed mainly by means of STOELTZNER's method (1905) (Cf. also WALLIN 1956). Fur the purposes of control methods according to v. KOSSA, HELLER-STEINBERG (1951), DAHL (1950), and MCGEE-RUSSEL (1955) have been used.

For the detection of possibly occurring mucopolysaccharides reactions for chromotropic and PAS-positive substances have been carried out. The identification of metachromatic substances has been performed according to LISON-SYLVÉN (GLICK 1951). The occurrence of mucopolysaccharides has been demonstrated mainly with the PAS-method of HOTCHKISS (GLICK 1951), in some cases according to BAUER-FEULGEN (GLICK 1951).

Results and discussion. The results have been assembled in Table 1. STOELTZNER's method differentiates calcified tissue, recently calcified portions being coloured black, older portions light-brown. This permits the distinction in the osseous layer of three zones with respect to the degree of calcification (Plate 1). Outermost is found an osseoid zone, followed by a strongly stained zone in which calcification is going on. The rest of the scale is stained light-brown, indicating that in this portion the calcification is terminated.

By reason of the fact that the osseoid zone lacks metachromasy and is PAS-negative it consists of "unripe" collagen, i.e. of fibrils and fibres with no or only a small amount of acid mucopolysaccharides in the cement matter (Plate 4). The strong metachromasy of the zone of calcification which indicates a concentration of acid mucopolysaccharides entirely agrees with the results obtained with bone by DZIEWIATKOWSKY, HELLER-STEINBERG, and RUBIN and HOWARD. Ca^{++} is probably bound to the two SO_2- and COOH--groups in the mucopolysaccarides. Since the methachromasy is caused by the SO_2-groups, and perhaps also by the COOH-groups, it disappears after the binding of Ca^{++} to these acid groups. After decalcification which results in the exposure of the acid groups the entire osseous layer becomes metachromatic (Plate 5).

Two possible explanations can be proposed of the strong staining of the zone of calcification with STOELTZNER's method. In the outer edge of the zone the first calcoglobulae can be seen as black islands in the osseoid. Farther inwards they turn into a continuous grainy structure. The stain can therefore depend on the relatively larger surfaces of the mineral complexes prior to their fusion into the final substance of the scale.

The staining can, on the other hand, depend upon a high concentration of PO_4-groups. During the demonstrations of bone salts according to STOELTZNER a binding takes place first between PO_4-groups and Co^{++}, and later between Co^{++} and S^{--}. It has been mentioned above (p. 000) that the zone of calcification contains the phosphate groups in higher concentrations than the entirely calcified bone. For this reason STOELTZNER's reaction ought to give a more pronounced effect for the free phosphate groups which later are bound by the Ca-ions. Analogously the metachromasy is an expression of the high concentration of acid groups in the zone of calcification. This interpretation is supported by the observations by CAGLIOTTI, ASCENCI, and SCROCCO (1954) to the effect that calcium-ions are bound to the osseoid via SO_2- and PO_4-groups.

The Fibrillary Plate

Introduction. The most important results of earlier investigations into the formation, development, and structure of the fibrillary plate have been accounted for on pp. 388—390. Very divergent opinions have been expressed about the origin of the fibrous layer, e.g. from SETNA's conception that the lamellae are secreted by the cells to KLAATSCH's and NEAVE's assumption that layers derived from the underlying dermis are incorporated with the scale as lamellae. Also the determinations of the chronological sequence for the formation of the fibrillary plate and the osseous layer, respectively, differ, PEVSNER considering that the formation of the fibrillary plate precedes that of the osseous layer, while NEAVE is of the contrary opinion.

Exposition of the problem. Since several important problems in connection with the formation of the fibrillary plate are still expecting their final solution, they have been taken up for renewed examination, partly with methods which had not been applied so far. The origin of the lamellae stands in the limelight. In case they are produced by cells the next question is, whether or not there exists a connection with the osseous layer as a whole and with the formation of the striae. The course of the calcification and the possible occurrence of mucopolysaccharides have so far not been the object of investigation.

Methods. The fibrillary plate has been generally stained with Heidenhain's Azan and with methyl green-pyronine in order to show active protein--producing cells. The process of calcification has been traced by staining with toluidine blue and according to STOELTZNER. Mucopolysaccharides have been shown by means of the Hotchkiss periodic acid-Schiff procedure (Hotchkiss PAS-reaction).

Staining with Heidenhain's Azan and with methyl green-pyronine

In order to obtain a general view of the morphology of the fibrillary plate sections (8—10 μ) were stained with Heidenhain's Azan. It was found possible to verify the main features in the structure of the fibrillary plate as reported by earlier authors.

Previously (SAVAGE 1919, SCHMIDT 1924) a connection between lamellae and striae had been denied. For this reason a series of counts of lamellae and striae in sections has been carried out. It could be established that two striae are formed upon the osseous layer while one lamella is developed in the fibrillary plate (LINDAHL and WALLIN 1955. For the more complicated conditions in the vicinity of a radius, see below, p. 405). The existence of a connection between the formation of striae and lamellae finds additional support in the fact that the diameter of the innermost lamella is always smaller than the diameter of the innermost stria, i.e. that the formation of the first stria is accompanied by the appearance of the first lamella.

When whole objects were stained the occurrence of a layer of cells immediately below the youngest lamella could occasionally be observed. These cells were stained with methyl green-pyronine in order to decide whether or not these cells exhibited signs of the synthesis of proteins. Among a material of 35 scales derived from three fishes only four cells were underlain by active cells. This indicates that the active stage is of short duration, and that the formation of lamellae is thus a periodic phenomenon (LINDAHL and WALLIN).

For the periodic formation of lamellae two possible explanations can be considered. It can depend on periodic alternations between active protein-producing and intercalated inactive phases experienced by one and the same layer of cells. It is, however, more probable that new layers of cells are successively developed. The production of a lamella by such a layer is followed by a period of inactivity during which the transformation of a new layer of cells from the dermis takes place.

The inorganic component of the fibrillary plate

The extent of the calcification has been examined mainly with the aid of STOELTZNER's reaction (See also WALLIN 1956). As a rule more than half of the thickness of the fibrillary plate is calcified. The border line between calcified and uncalcified material obliquely crosses the lamellae. Thus the age of the individual lamella is of no importance for the possibility of its becoming calcified.

Under high magnification the boundary is seen to have a grainy irregular structure (Plate 6). The grains are formed by crystallites lacking by their size counterparts in the osseous layer. These crystallites can be seen also in preparations of entire scales, where they appear with particular clearness at the erosion borders of scales in resorbtion (Plate 7). They are orientated along the fibrils, and probably embedded between them in the lamellae.

From the limit of calcification larger mineral complexes, so-called Mandlian bodies, penetrate into the uncalcified material. Their edges have the same grainy structure as the rest of the limit of calcification, and they clearly are built up of crystallites.

Under a magnifier thin layers of the fibrillary plate down to the thickness of a few lamellae can be separated. On treatment with hydrochloric acid the lamellae inclusive of the Mandlian bodies are decalcified. During this process gas is liberated, pointing to calcium carbonate as material of the crystallites. No special structure in the fibres can be distinguished in the places from which Mandlian bodies had been removed.

PEVSNER interprets the Mandlian bodies as degenerated cells which on their disintegration add elastin to the fibrillary plate. Thus she does not connect the bodies with the mineral component. SCHMIDT (1947) on the contrary supposes that they originate by a fast precipitation of crystallites.

In addition to the youngest lamellae the present writer finds also regions below the radii of the osseous layer to be uncalcified (Plate 8). A section through the central portions of a scale therefore exhibits a series of conical uncalcified regions which at the bottom of the plate merge into the collagenous lamellae.

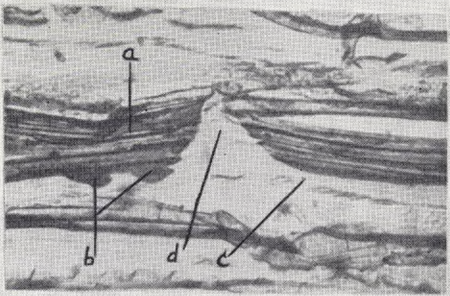
NEAVE does not deal with the calcification of the fibrillary plate. He considers it probable that the fibrillary plate is formed initially as collagen which is later infiltrated with ichthylepidin. Histologically he demonstrates the youngest part of the plate together with a wedge-shaped region under each radius to consist of collagen, and finds that the remainder of the fibre plate contains also ichtylepidin. There is complete agreement between NEAVE's descriptions and the above mentioned determinations of the extent of the calcification in the text as well as in the figures. Since there exists no doubt that the fibrillary plate contains an inorganic component, and that the extent of this component can be determined with the aid of STOELTZNER's reaction, it appears probable that the "ichtylepidin boundary" discovered by NEAVE is in reality the boundary of the calcification.

Staining with toluidine blue

For the identification of metachromatic substances staining with toluidine blue according to LISON-SYLVÉN was used. The most important results are assembled in Table 1.

Table 1 shows that no part of the fibrillary plate exhibits metachromasy. This is astonishing as metachromasy is a typical indication for calcification of the osseous layer. From a wider point of view it is even more surprising, since RUBIN and HOWARD (1950) report metachromatic substances in all examined calcified objects with the exception of pathological calcification of the types of ureate and stearate stones. This makes the fibrillary plate, considered as a calcified structure, a unique object in the animal kingdom.

Orthochromasy is distinguishing for acid substances in which the negatively charged groups are not situated sufficiently close to each other to cause metachromasy. The orthochromasy which disappears with calcification, and which does not return after decalcification indicates that acid groups in the



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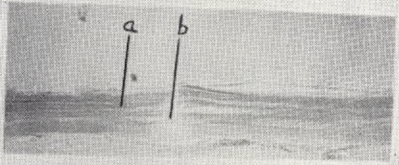

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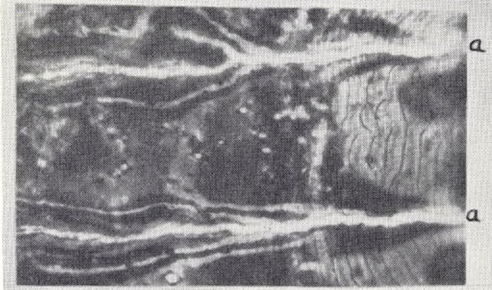

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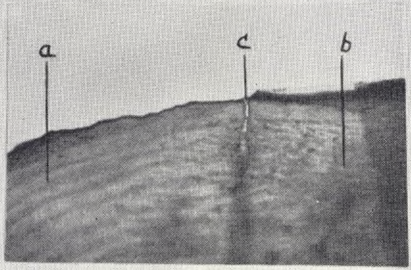

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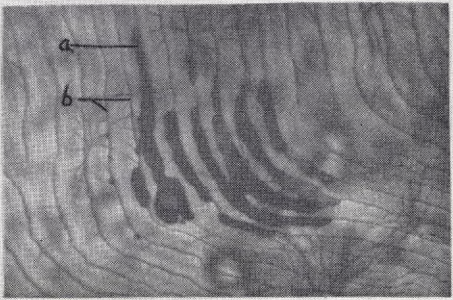

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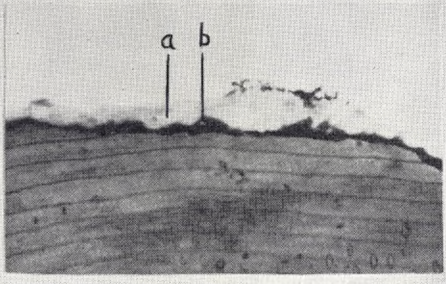

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Plate 8. Section through scale of roach. STOELTZNER. a = calcified lamellae, b = Mandlian bodies, c = uncalcified lamellae, d = radius. × 565.

Plate 9. Section through scale of roach. HOTCHKISS' PAS-reaction. a = fibrillary plate, b = radius. × 385.

Plate 10. Extensions from the lamellae along the radii. STOELTZNER. Polarized light. Focus of the scale beyond left margin of the picture. a = radii; around them extensions from lamellae situated nearer the focus are seen as alternatingly light and dark bands. × 230.

collagen or in the cement matter surrounding the collagen are removed or neutralized before the mineral is introduced. It is an interesting fact that the regions below the radii which remain uncalcified are also devoid of orthochromasy.

The occurrence in the periphery of the osseous layer of metachromatic substances which are absent in the fibrillary plate makes possible the demonstration of a close connection between the two components of the scale in the germ stage. Plate 4 shows a section through the periphery of a scale. The metachromatic zone of calcification (b) penetrates into the osseoid zone (a) which is surrounded by active cells. Below the former a direct transition is found between the osseoid zone and the youngest part of the fibrillary plate. This shows that the osseous layer and the fibrillary plate have the same origin, and since in certain cases also a continuous layer of pyroninophilic cells surrounds the osseoid zone, and underlies the fibrillary plate, the origin of the latter as a cellular product is thereby made very probable. NEAVE's hypothesis that layers of the dermis are incorporated with the plate was based upon the discovery of cells which disappear when the first lamella has been formed. The above mentioned periodic activity is therefore probably of short duration in comparison with the intervening periods of inactivity. This circumstance together with the use of a less suitable method can perhaps explain NEAVE's failure to demonstrate cells below the fibre plate.

The first indication of a differentiation of the osseoid zone into osseous layer and fibrillary plate thus consists of a chemical change which is histochemically expressed by metachromasy. This change can be imagined to have originated mainly in one of two ways: Either can acid substances be formed at the ripening of the osseoid, or acid groups can originally have been blocked up in order to be liberated only later on. The boundary between the metachromatic region and the presumptive fibrillary plate is, however, very smooth, and runs parallel with the lower surface of the plate which circumstance might be connected with an observed sub-microscopical dissimilarity in the structure (see below).

Hotchkiss' PAS-reaction

The zone of calcification and the completely calcified osseous layer are strongly PAS-positive (Table 1). This suggests that the occurrence of

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Plate 11. Resorption of edge of scale, interrupted at the radius on the boundary between exposed and unexposed scale. STOELTZNER. a = unexposed part of scale, b = exposed part of scale, c = radius. × 220.

Plate 12. Resorption of surface of the osseous layer. STOELTZNER. a = resorption, b = striae. Note the incipient resorption on the tops of the ridges of the striae. × 310.

Plate 13. Strong resorption of edge of scale. STOELTZNER. a = osseoid zone, b = zone of resorption. × 220.

Table 1. Reactions on mucopolysaccharides and state of calcification of the roachscale.

	Ortho-chromasy	*Metachromasy*	*PAS-reaction*	*Reaction for bone salts*
Osseous layer				
I. Normal scales				
a) Osseoid	0	0	0	0
b) Zone of calcification	0	+++	+++	+++
c) The calcified remainder	0	0	+++	0—+
II. Regenerated scales				
a) Osseoid	0	++	+	0
b) Zone of calcification	0	+++	++	+++
c) The calcified remainder	0—+	0	++	++
The fibrillary plate				
I. Normal scales				
a) Uncalcified lamellae	+++	0	+++	0
b) Calcified lamellae	0	0	+++	++
II. Regenerated scales	0	0	0	0

Explanation of symbols: +++ strong reaction; ++ moderate reaction; + feeble reaction; 0 no reaction.

mucopolysaccharides is coordinated with the calcification. Also the fibrillary plate gives a positive result, but the intensity of the reaction is the same before and after calcification. The result is negative below the radii (Plate 9) and, frequently, in the youngest lamellae. The fact that the distribution of orthochromasy coincides with that of the PAS-positive structure renders probable that the acid groups enter into the mucopolysaccharides. Thus the calcification requires the presence of mucopolysaccharides, as in the osseous layer. The intensity of the PAS-reaction is approximately the same in both layers.

Arrangement and origin of the fibres

The arrangement of the fibres has been examined in polarized light in entire objects stained according to STOELTZNER, and in sections stained with toluidine blue. According to earlier views a lamella is a unit of parallelly arranged bundles of fibres which only in the periphery curve along the edge of the scale. With the aid of the polarization microscope a modification of this structure has been established (Plate 10). By their parallel arrangement in a lamella the fibres turn the polarized light, and appear luminous when they include a certain angle with the plane of oscillation of the polarized light. Another neighbouring lamella is at the same time dark, since its fibres include another angle with the above-mentioned plane.

The alternatingly light and dark bands along the radii are due to small excrescences of the lamellae. Between the radii the peripheries of the lamellae are closer to the centre of the scale, and narrow extensions of the lamellae continue in the direction of the radii only at the latter. Thus the growth-limiting factor which induces the formation of *one* lamella for every two radii in the osseous layer is absent at the radii. This factor can be of a mechanical nature. To judge from the direction of the fibres at the edge the latter is subject to a pressure perpendicular to the periphery. The deflection of the fibres in the periphery into a direction more or less parallel with the edge of the scale ought likewise to represent a response to this pressure. This pressure seems, however, to be missing at the radii, and for this reason extensions of the lamellae are able to continue their growth towards the edge of the scale. Apart from the foregoing nothing can be said about the time and the way of the formation of the extensions.

In thin sections the outermost fibres can as a rule be discovered inside the outermost stria. They give the impression of gradually increasing in thickness towards the centre of the scale. In one case a very feeble double refraction has been observed in the osseoid zone outside the presumptive stria in a series of closely situated thin sections. This seems, however, to constitute an exception. Thus the formation of the fibres and, together with them, of the lamellae and the calcification take place about simultaneously in the periphery of the scale.

From the above we can derive a sub-microscopic arrangement of the fibres. To this we can refer the differentiation of the metachromatic zone of calcification and of the underlying lamella. The fibres of the osseoid which are destined to enter into the osseous layer are arranged strictly parallel with the edge of the scale. The metachromatic cement matter is gradually formed around these collagenous fibres. The lower surface of the zone of calcification is smooth and parallel with the lower surface of the scale, where it meets the future fibrillary plate in which the fibrous structure is still absent or feebly developed. Bundles of fibres are formed in the lamellae only after the passage of the zone of calcification of the osseous layer.

Summary

Earlier investigations have established the lamellar structure of the fibrillary plate, the change in the direction of the fibres in different lamellae, and the fact that below the radii of the osseous layer the fibrillary plate has a different chemical structure. These observations have been supplemented by the present investigation. It seems extremely probable that not only the osseous layer but also the fibrillary plate is produced by cells. A still more intimate interrelation between the two structures has been established near the edge of the scale, where both fibrillary plate and osseous layer originate from the same osseoid zone. The formation of fibres and with it the first formation of lamellae takes place as a rule at the 1st—2nd stria, counted

from the edge, and is governed in such a way that the formation of two striae corresponds to the simultaneous formation of one lamella. The governing factor could not be identified. It is absent at the radii, where narrow extensions of the lamellae continue to grow after the main part of the lamella has ceased growing.

The greater part of the fibrillary plate is calcified. The mineral component is present in the form of crystallites, arranged along the fibres. Acid mucopolysaccharides of the type observed in the osseous layer are absent. Mucopolysaccharides, necessary for the calcification, and containing a lower concentration of acid groups, have been identified. No calcification takes place in the radii, where they are missing.

Regeneration of Scales in the Roach

Introduction. For a long time the fast replacement of lost scales in fishes has aroused interest (FRAISSE 1885,[1] MORGAN 1900). The characteristic appearance of these scales was the reason of observation and description already before their earlier history was known (HOFFBAUER 1900[1]). Histological investigations have been carried out in later times amongst others by SAUTER (1934), NARDI (1935), WUNDER and SCHIMKE (1935), NEAVE (1940), and WUNDER (1949).

This investigation into the regeneration of the scales was intended to trace the development of the scales of the fishes from the germ stage to the final stage. The formation and morphology of a regenerated scale differs in important respects from those of the normal scale, but the main features must, nevertheless, be taken to be roughly the same. The study of the regenerated scale affords, however, several advantages; on the one hand several of the reactions of the cells are more vigorous and thereby more easily observable, on the other hand can a certain stage easily be obtained for examination, once a time scale has been established. In addition to an examination of these conditions it was intended to control certain statements in the literature with the aid of new methods.

Material and methods. The investigation has been carried out on roaches of 8—12 cm length. The fishes were transferred from storage aquaria to laboratory aquaria in which the temperature was allowed to rise from about 8° C to 19°—20° C in the course of 48 hours. The regeneration has thus taken place at the higher temperature. All scales were removed from a surface of about 4 cm^2 upon the side of the fish. The regeneration was controlled after 1, 2, 4, 6, 8, and 18 days. In one case the wound was examined immediately after the removal of the scales.

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[1] Quoted after WUNDER (1949).

After fixation in absolute alcohol the objects were desiccated and embedded in paraffin in the general way, and cut into sections of 8 μ thickness. Staining was carried out with Heidenhain's Azan, methyl green-pyronine, and toluidine blue. The reaction according to STOELTZNER was carried out for bone salts, and according to HOTCHKISS for the detection of mucopolysaccharides.

A series of experiments has been carried out with cutting of the edges of the scales. In certain cases a larger or smaller portion of the exposed part of the scale was cut off, in others a sector was snipped out between or around radii. With these experiments it was intended to follow the regeneration from the edge of the wound, and to compare the arrangement of the striae formed in this connection with those formed upon portions of the scale in closest proximity with the field of regeneration. It was intended also to study the importance which the radii might have as transporting organs.

Observations. Sections through the skin prepared immediately after the removal of the scales show that most of the epidermis is missing. The dermis has remained practically intact. After *24 hours* the scale pockets had been filled with an exudate in the shape of a granular mass. The place of the epidermis is occupied by a dense, fairly homogeneous "crust". Already after *48 hours* regeneration has led to remarkable results. New epidermis is being formed as a thin layer. The amount of the granular mass in the scale pockets has been reduced, and the cytoplasm of the cells at the bottom of the pockets exhibits a feeble pyroninophilia.

After *96 hours* well developed agglomerations of cells have been formed, which are separated from each other, and exhibit strong pyroninophilia. In some cases the formation of scales has started, and extracellular material has been deposited. After *six* days long strands of metachromatic spiculae have been formed. Their calcification has begun.

Eight days after the begin of the regeneration the activity has ceased in the central groups of cells. Only the peripheral groups of cells in the scale pocket continue to grow. The edge of the scale is fibrous and loose, occasionally the material of the scale can be seen to have direct connection with osteoblastlike cells (Plate 2). Around the edge the cells are perpendicularly arranged, and merge into a layer of pyroninophilic cells extending below the entire scale. Below this layer another layer is found the cells of which are in the stage of differentiation. The fibrillary plate is being formed. As it is not stained by any of the used reagents it probably consists only of fibres without surrounding mucopolysaccharides. In the connective tissue outside the edge af the scale longish fibroblasts can be seen to become increasingly pyroninophilic while the growing scale approaches. In this connection they assume a more contracted shape, and become cylindrical at the periphery of the scale. Upon the upper surface of the scale the cells have lost most of their pyroninophilia, and part of them is inclosed in the osseous layer.

After *18* days the scale has penetrated into the epidermis which is pushed before it. The edge of the scale is surrounded by active cells. The fibrillary plate consists of several layers, but is not calcified, and is underlain by active cells.

The fishes in which parts of the scales had been removed could be controlled during about $^1/_2$ year at a temperature of 8°—10° C. No change took place at the cut edge. At the above temperature completely removed scales are replaced within about one month. In fishes which were kept after the operation at 18°—20° C the scale was resorbed instead of being regenerated as had been expected. This happened both when a whole portion had been removed, and when a notch had been cut into the scale.

Discussion. SAUTER (1934) demonstrates that the scale is regenerated within small groups of cells. The fact that the regenerative cells by their shape and arrangement produce the impression of "flowing" makes him believe that they migrate. This applies obviously only to cells in the neighbourhood of an already existing regenerate.

The cells which give rise to the first agglomerations, and which exhibit a feeble pyroninophilia (the 48-hour stage) are differentiated from the bottom of the scale pocket. In appearance they agree entirely with the cells in differentiation outside the edge of the scale, which are here described under the 8-day stage, and which had been considered as migratory by SAUTER. As an alternative to his conception we can therefore, partly in agreement with NEAVE, suppose that the regenerative cells are differentiated *in situ*. Simultaneously with an increase in the pyroninophilia of the plasm the originally elongatedly fusiform fibroblasts contract, and assume the appearance which is typical for active cells. The impulse towards this differentiation comes in the first stage from the wounded surface in the scale pocket, later probably from the growing regenerate.

Instructive pictures of the first formation by the scale of strongly pyroninophilic cells which surround its two sides are obtained especially from the 6—8 days stage. Here the extracellular material can be seen to leave the cell plasm, and to change into the matrix of the scale (Plate 2). The same cells which contribute to the formation of the osseous layer at the edge of the scale are still active, when the first lamella of the fibrillary plate can be discerned. This observation entirely agrees with, and supports the previously demonstrated differentiation of the osseous layer as well as of the fibrillary plate from one and the same osseoid zone. SAUTER's assertion to the effect that the two components of the scale are derived from different layers of cells can thus not be substantiated. NEAVE's hypothesis that the dermis is directly incorporated with the scale as lamellae must be refuted once more. The observation of a layer of active cells together with an underlying layer of cells in course of differentiation below the fibrillary plate in the 8-day stage, together with that of active cells below a plate consisting of several lamellae points to the successive development of lamellae from cells derived from the dermis (cf. p. 400).

The course of the calcification differs from that in normal scales (Table 1). The osseoid zone exhibits a moderate metachromasy right to the periphery and a feeble PAS-reaction. Thus the osseoid "ripens" immediately after its formation. The zone of calcification and often also the osseoid are considerably broader than in normal scales. This ought to be due to the faster growth of the regenerating scale.

The calcified regenerated scale exhibits as a rule a feeble orthochromasy and a moderate phosphate reaction. These features point to under-saturation with calcium ions, i.e. the scale is not completely calcified.

WUNDER (1949) describes the regenerated scale as consisting of a central, enlarged centre of growth with reticular structure, surrounded in the periphery by striae. For the origin of this structure he offers no explanation. The problem had, however, been solved already be NEAVE whose results have been confirmed by this investigation. The scale is not developed from a single centre of regeneration, but from a large number of fusing regenerates. Each group of cells, described for the 4—6 days stage, represents such a regenerate. When they meet, growth ceases, and a furrow homologous with a radius is formed between them. (Cf. p. 419 ff.).

Upon examination of cut scales in fishes kept at low temperature it could be found that at the cut edge no active cells were formed by transformation of their fusiform mesenchymatic predecessors. For the induction of a regeneration it is obviously necessary that a greater portion of the scale be removed.

The Importance of Vitamin C for the Formation of Scales

Introduction. It is generally assumed that most animals, the fishes included, are able to supply themselves by synthesis their requirements of vitamin C. In spite of this it has been shown that the healing of fractures, e.g. in rabbits, is delayed if the animals at the same time are fed a diet without vitamin C (HANKE 1935,[1] 1936,[1] LAUBER 1936,[1] LAUBER and other 1937,[1] GIANGROSSO 1939,[1] GIANGROSSO and GANGANTINO 1939[1]). After breeding experiments with fishes HAEMPEL (1927) is of the opinion that for a normal growth all known vitamins are necessary.

In spite of the fact that the function of vitamin C in the animal body is to the greatest part unknown, the damages due to C-avitaminosis are well studied. Certain specialized cells, like fibroblasts, osteoblasts, and odontoblasts, cease to form collagen, osseoid, and dentine, respectively (FOLLIS 1951). In addition to the loss of the ability to form extracellular fibres the

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[1] Quoted after Bourne (1956).

incorporation of sulphate with chondroitin sulphate is reduced to one third of what is normal (REDDI and NORSTRÖM 1954). Also the differentiation of the above mentioned cells from their mesenchymal predecessors ceases (FOLLIS 1951).

As the regeneration of the scales of fishes implies a fast production of extracellular material, this process ought to be usable with advantage for the establishment of a possible C-avitaminosis in fishes. With regard to our present knowledge of the symptoms of C-avitaminosis it ought in fact to represent the most sensitive method.

Material and methods. The experiments were carried out with roaches. On them upon a surface of about 4 cm^2 all scales were removed, whereupon regeneration took place in cold water or in water of room temperature, at 8° and 18°—20° C, respectively. Before and during the period covered by the experiments the animals were fed a diet without vitamin. C. This consisted of cheese, which according to information received from the Govt. Institute for Popular Health represents a perfectly adequate food completely free of vitamin C, together with a synthetic diet according to HARRIS and RAY (1932). In the way of ordinary routine the regenerates were sectioned and stained with methyl green-pyronine.

Results and discussion. Comparisons between scale regenerates from experimentally treated animals and their controls reveal differences of such a kind that C-avitaminosis must be assumed in the former. A typical feature is the delay in the differentiation of the cells, followed by a slow production of extracellular material. After the differentiation the active cells do not assemble in the above mentioned groups of cells, but occur thinly spread. This leads to a regenerate of more porous structure, often with enclosed cells. In certain cases no intercellular material has been formed at all. The cells are then rather strongly pyroninophilic, but have retained the fusiform shape which is typical for inactive cells.

Since these orientating experiments are not in line with the main aim of the investigations they have been carried out only on a small scale. The results have therefore to be considered as preliminary. The method ought, however, to have a certain value both on account of its great sensitivity and its comparatively easy application. For this reason it ought to be suitable for experiments on a larger scale.

Resorption of Scales caused by Lack of Vitamin D and Ensuing Regeneration

Introduction. It is a well-known fact that the scales of the salmon are subject to reduction during the migration of the fish from the sea to the spawning places. CRICHTON (1935) describes, how the resorption begins laterally, and then continues around the edge of the scale. Also the resorbtion of the osseous layer upon the surface of the scale has been observed. The resorption goes on as long as the salmon remains in fresh water. The probable explanation is that the salmon during his migration consumes only an inconsiderable amount of food, and uses the resorbed tissues, scales, connective tissue, etc. in metabolism and for the building up of the sexual products.

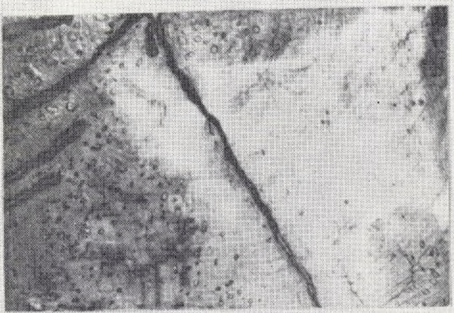
Also the scales of the roach undergo resorption, though in a lesser degree than those of the salmon. MASTERMAN (1923) is of the opinion that the resorption takes place during autumn and winter at the end of the period of growth, and that it thus is not a spawning mark. JONES (1953) on the other hand finds the resorption to take place shortly after the spawning, and that scales are resorbed only in sexually mature fish or fish which has spawned. This leads him to the conclusion that the resorption in the roach is a spawning mark quite comparable with that in the salmon.

All these observations have been made on captive fish. As nothing is known about the course of the resorption and the subsequent regeneration, experiments have been carried out with fish in aquaria were these processes could be followed step by step.

Material and methods. All experiments have been carried out with roaches. For the purpose of inducing resorbtion of the scales the experimentation animals have been fed a rachitogenic diet according to STEENBOCK-BLACK (1925) with a addition of salts of calcium and strontium (SOBEL, COHEN, and KRAMER 1935). The fishes exhibited no distaste to the synthetic diet so that the results can not be the consequence of malnutrition. The control animals were fed with liver pie. The temperature of the water was kept at 17°—19° C. The scales were stained according to STOELTZNER.

Observations. After about three weeks the resorption is quite obvious in most experimentation fishes. In younger specimens it is in general of smaller extent. Usually the resorption begins at the edge of the scale between the antero-lateral corners and the limit between the exposed and the unexposed part of the scale. It then spreads to the cranial edge of the scale. It is characteristic that the resorption rarely attacks the exposed part of the scale. Even when the resorbtion is strong at the lateral edge, it nevertheless ends almost without exception at the radii which reach the periphery at the mentioned limit (Plate 11).

The resorption is introduced by the formation of a dark-coloured inward bulge from the zone of calcification. Upon this stage the osseoid is still unaltered. The grainy structure of the zone of calcification is followed by a considerably narrower deep-black edge along which the resorption takes place. The edge wanders inwards while at the same time the mineral component is dissolved. Often the osseoid devoid of mineral substance is not resorbed at the same speed, but a broad border of osseoid remains outside the zone of resorption.



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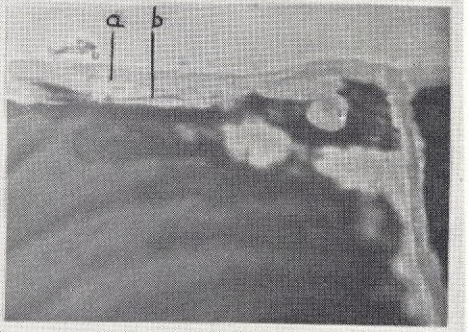

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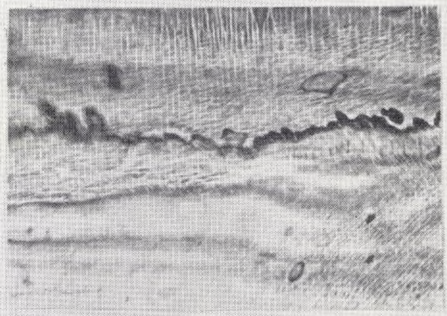

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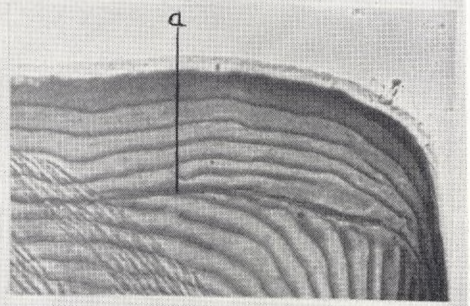

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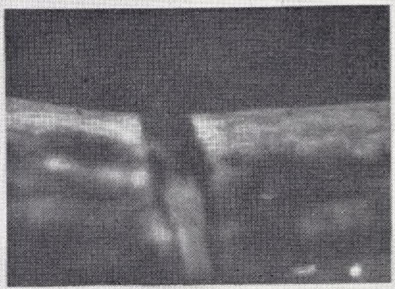

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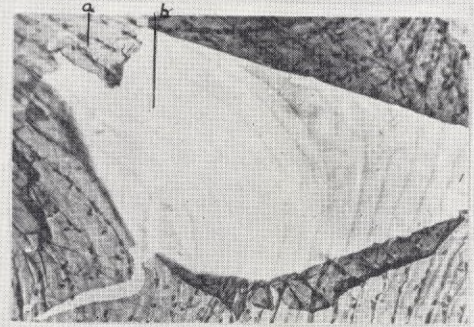

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Plate 14. Fibrillary plate with locally darkened portions prior to resorption. STOELTZNER. Note the abundant occurrence of Mandlian bodies in the darker portions of the fibrillary plate. × 100.

Plate 15. Incipient regeneration of resorbed edge of scale. STOELTZNER. a = osseoid zone, b = stria under first formation. × 720.

In many cases the observation has been made that the resorbtion of the osseous layer follows principally the crests of the striae. This happens almost without exception at resorption within the surface of the osseous layer, where also the first introduction of resorbtion appears upon the summit of a stria (Plate 12). This type of resorption often takes place in connection with radii.

The fibrillary plate is resorbed at about the same rate as the osseous layer. In a number of cases mineralized fibres are left behind in the osseoid, in other cases the fibrillary plate is resorbed earlier than the osseous layer. Also here the resorbtion is introduced by a darkening of the tissue. In the areas predestined for resorbtion a tendency towards an increase in the number of the Mandlian bodies has been observed (Plate 14).

In no case have recently regenerated scales been affected by resorbtion. The regeneration also goes on simultaneously with the resorption of surrounding scales.

When the experimentation fishes are put on normal diet again, it takes about 10—14 days, before the first signs of regeneration can be discovered at the disintegrated edge of the scale. The regeneration is characterized by the fact that both osseoid and zone of calcification are broader than in the case of normal formation of scales. The rate of growth slows down only when the scale approaches its original size. Otherwise the formation of new scale material takes place in the above described way. (For the formation of striae, see p. 431).

Only after the development of at least 2—3 striae the first lamella of the fibre plate is differentiated below the regenerated osseous layer. During the calcification a dense collection of Mandlian bodies is formed in the joint between the original fibre plate and the newly formed lamella (Plate 16).

The experimentation fishes which were fed a strontium-rachitogenic diet were attacked by the resorbtion of the scales to the same extent as the fishes

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Plate 16. Boundary between the original fibrillary plate and fibrillary plate regenerated after resorption. STOELTZNER. Note also the distinct crystallites and the Mandlian bodies. × 640.

Plate 17. Edge of scale, completely regenerated after resorption. STOELTZNER. a = limit of resorption. × 240.

Plate 18. Edge of scale with radius. Whole mount from which the minerals and mucopolysaccharides have been removed. In the periphery of the scale luminous strands of collagenous fibres are seen in the futur osseous layer. These strands are suddenly interrupted in the centre of the picture, where a radius runs out. This is dark most outwardly, i.e. no boundles of fibres have as yet been formed in the underlying lamella. The first luminous fibres in the lamella are situated immediatly inside the outermost stria. × 660.

Plate 19. Scale of roach with flakes loosening from the surface layer. Gallocyanine-chrome alum. a = surface layer with cells, b = the exposed internal substance. × 245.

mentioned above. These animals died in all cases during the earlier stages of the experiments, making the study of the regeneration of the scales impossible.

Resorption occurred occasionally also among the control animals. In all cases it healed after a short time, differing thereby from the resorption in the experimentation fishes which was suspended only after the animals had been given adequate food.

Discussion. These experiments show that also in fishes the mineral metabolism is disturbed by a lack of vitamin D. This possibility has been mentioned already earlier (SCHÄPERCLAUS 1941), but the writer is not aware of any attempts at an experimental treatment of the problem. He has not been able to verify the resorbtion of the opercula of the gills, described by SCHÄPERCLAUS.

Initially the mineral is dissolved from the bony tissue, and then only also the organic component is resorbed. This points to a disturbance in the calcium-phosphorus metabolism of the fish. No explanation can be offered of the fact that only fishes of a size greater than approximately 6 cm are subject to this disturbance. The observation agrees, however, with the findings by Jones on fishes caught in natural surroundings. The writer has, however, established that also fishes affected by parasitizing Ligula fall victims to the resorption of scales, which is denied by this author.

As the resorption appears temporarily with the control fishes irrespective of the season it is not necessarily connected with the spawning. It is more tempting to assume that the metabolism of the fish is thrown out of balance by the rise of temperature in the aquarium, in order to adjust itself gradually to the faster metabolism induced. This is in good agreement with JONES' conception that in roaches caught in their natural surroundings the resorption takes place in midsummer. According to TESCH (1955) the fishes undergo at this time a period of hunger. Here the disturbance of the mineral metabolism is obviously only one part of a more extensive complex. Yet its results are the most easily observable.

Serum Calcium in Normal Roaches and in Roaches Injected with AT 10

Introduction. So far it has not been possible to prove with certainty the occurrence of parathyroid glands in fishes. Such glands are found within all other groups of vertebrates. Already in 1940 SCHERESCHEWSKY discovered in the gill region a glandular epithelium which she suspected to be a parathyreoid. PICKFORD (1953) proposes that the parathyreoid of fishes is governed by the hypophysis which should be stimulated in turn by light impulses via the epiphysis. This hypothesis would be able to explain the discovery by RASQUIN and ROSENBLOM (1953)[1] that in fishes kept in darkness the skeleton becomes decalcified. An ultimobranchial gland, supposed by these authors to correspond to the parathyreoid, is strongly hypertrophied. PICKFORD's hypothesis is supported also by the discovery by PFLUGFELDER (1953) of epiphysectomy as cause of skeletal deformations.

In order to establish whether or not the roach keeps the content of calcium in the blood stabilized within the same narrow limits as higher animals the content of serum calcium has been determined. The concentration of serum calcium has been examined also after injection of the fish with AT 10, an anti-tetanic drug which acts similar to the parathyreoid extract. The results of this part of the investigation ought to give information, partly whether or not the calcium metabolism in the roach is governed in a way similar to that in higher animals, and partly also whether or not this fish reacts to a preparation of the character of the parathyroid hormone in a way resembling that of other vertebrates.

Experimental remarks. The experiments were carried on from the middle of February to the middle of March on roaches of 12—18 cm length. The determination of the serum calcium was made according to the micromethod of BIERING (1944) which permits analyses on individual fishes.

AT 10 was intraperitoneally injected, whereby in some cases a puncture of the intestine was observed. Blood was obtained from the fishes by cutting off the axis of the tail. From each fish 0,1—0,2 ml serum was obtained which sufficed for the method in question. This was controlled with a solution of Ca^{++} of known concentration as a standard. The reported results have been corrected with regard to the control. In several cases the blood of the experimentation fishes was observed to coagulate at a faster rate than that of normal fishes.

Discussion. In the course of a general examination of the blood of the carp DOMBROWSKI (1953) obtained in four determinations of the serum calcium values between 11.31 mg⁰/₀ and 28.8 mg⁰/₀. This great difference in the content of calcium in one and the same species creates the impression that the control of the calcium-phosphorus metabolism, present in higher animals, is absent here. The carp ought on the other hand to be more tolerant against changes in the concentration of calcium. Unfortunately the reader is not informed about the method used, neither does the author tell, whether or not the values had been obtained from individual fishes.

The results of the partial examination, here submitted, (see Table 2) with an observed maximal difference of 1,9 mg⁰/₀ fit, on the other hand, with the statements made by FONTAINE and PORTIER (1931). They found the maximal difference within one and the same species to amount to 1.5 mg⁰/₀, but also that there were considerable differences between different species. Their

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[1] Quoted after PICKFORD (1953).

Table 2. The normal content of serum-Ca in the roach and its change after injection with AT 10.

Normal content mg %	Amount of serum-Ca after injection	Injection ml	Activity mg/ml	Time between injection and test
9.3	13.3	0.1	0.054	48 hours
9.5	13.4	0.1	conc.	48 „
9.8	13.8	0.15	0.054	21 „
10.0	14.6	0.15	0.054	1 hour
10.3	14.6	0.15	0.054	1 „
10.4	15.4	0.15	0.054	30 min.
10.4	15.9	0.1	conc.	50 „
10.6	16.0	0.15	0.054	21 hours
10.6	16.6	0.15	0.054	30 min.
10.6	16.7	0.2	0.054	1 hour
10.9	15.03 ± 1.27			
10.9				
11.2				
10.35 ± 0.16				

The difference, 4.62, is significant.
T = 8.30 p 0.005

method demanded in general the mixing of the blood of several fishes before the determination. The size of the maximal difference found here together with the absence of a difference between the sexes indicates that in the roach the balance of calcium is kept within the same close limits as in higher animals.

McChesney and Giacomino (1945) have examined the effect of AT 10 on normal mammals as well as on mammals which had undergone parathyreoidectomy. In dogs they found 1 mg AT 10/kg of the weight of the body to cause an increase of serum calcium by about 4.5 mg$^0/_0$. Also in this case the reactions of the roach agree well with those shown for higher animals (See Table 2). The difference of the values from normal and injected fishes amounts to 4.6 mg$^0/_0$. The used dose is approximately the same as that employed with dogs. No higher values are obtained, if the same quantity of AT 10 is given, but in a higher concentration. The brief time of only thirty minutes required after the injections for the appearance of the new Ca^{++}-value is worthy of notice.

In summing up we can state that there exists no essential difference in the content of serum calcium between the normal fish and higher animals, nor between their way of reacting to a preparation of the character of the parathyroid hormone. There are thus good reasons for the assumption that the roach and probably also the other Teleostii posses a so far undiscovered parathyreoid gland or another organ with an identical function.

Some Observations on the Development of the Osseous Layer

Scales which had been deprived of minerals and mucopolysaccharides (RUTH 1946, 1947) have been examined in polarized light (Plate 18). The osseoid zone exhibits strong double refraction, and under higher magnifications fibres can be discerned. Similar to membranaceous bone in higher vertebrates the scale of fishes is built up of coarse fibres forming a network, so called "woven bone".

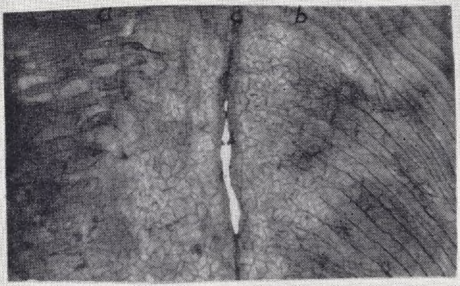
Under higher magnification the surface of the fully developed osseous layer appears extremely fine-grained in the ordinary microscope, and covers both the striae and the trough between them. This is distinctly seen when scales are examined under the electron microscope (SIGNER, V. BEUST, and CORTI 1951).

Basing himself upon observations under the polarizing microscope SCHMIDT (1951) is of the opinion that the scale of *Capros aper* consists of a, about 1 μ thick, limiting layer which forms a film upon the remaining homogeneous osseous layer. This limiting layer seems to lack collagen, and ought to be a phenomenon of limiting surfaces. He supposes it to be more strongly calcified than the rest of the osseous layer.

When scales of roaches are stained with gallocyanine-chromium alum frequently thin flakes are detached from a superficial layer of the osseous plate (Plate 19). These flakes are stained, but not so the surface of the exposed internal substance. The teeth of the striae are visible upon the flakes, whereas no corresponding structure is seen upon the striae formed of the internal substance. More rarely flakes are detached when entire scales are stained with other methods. The reaction for bone salts according to STOELTZNER produces stained flakes, while the internal substance remains unstained. Thus the light-brown colour imparted to the completely calcified part of the scale of the roach by treatment with STOELTZNER's method is localized exclusively to a thin surface layer.

In rare cases the surface layer can be missing. This has been observed upon the exposed part of the scale, where only the troughs between the striae are covered by a darker layer, whereas the striae are feebly coloured (Plate 20). In this case the crests of the striae are likewise without surface sculpture. They have smoother and more rounded shapes, and resemble to a high degree the striae as they had been exposed after the removal of the surface layer.

It appears probable that the thin layer which becomes detached at the above-mentioned reactions corresponds to the limiting layer shown by SCHMIDT with optical methods. In thin sections stained according to STOELTZNER and with toluidine blue a thin layer, possibly representing the limiting layer, is stained more intensely than the internal substance. This reaction



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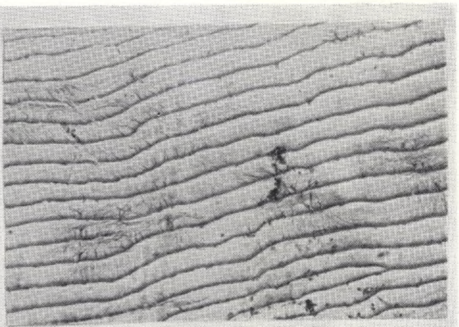

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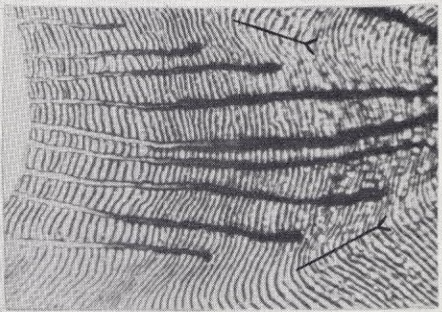

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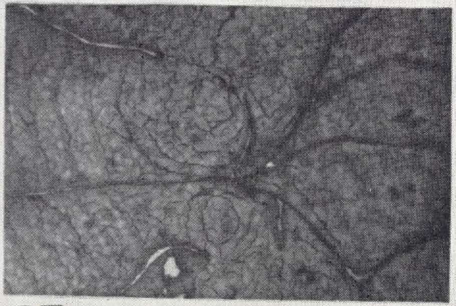

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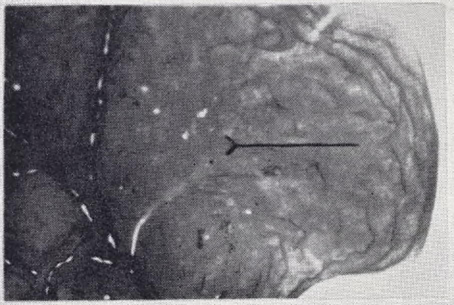

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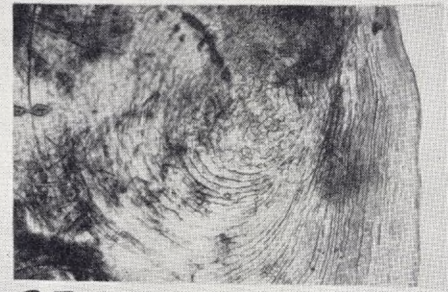

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Plate 20. Border area between the exposed and the unexposed part of the scale. STOLTZNER. a = exposed part, b = unexposed part, c = radius. × 200.

Plate 21. Bursts in osseous layer and fibre plate. STOELTZNER. The cracks of the osseous layer are best developed upon the crests of the striae, corresponding bursts in the fibrillary plate are seen as a dense network. × 225.

Plate 22. Radii from the cranial part af the scale. Dry-mounted whole mount. The arrows indicate the directions of vigorous growth of the scale. × 60.

and also the dark surfaces in the troughs of the entire, object point, however, to a lower degree of calcification of the surface layer than of the internal substance of the scale. According to a previously (p. 398) exposed hypothesis tissues with a lower concentration of bone salts ought to exhibit a darker colour than those in which the mineral component is present in a higher concentration.

It must, however, be considered an established fact that the osseous plate of the scale of the roach is overlain outermost by a surface layer which covers the internal substance.

It has not been possible to verify SCHMIDT's statement on the existence of a tubular layer underneath the surface layer.

In scales of *Rutilus rutilus* PEVSNER describes in the radii a system of tubes which branch out into a network in the osseous layer. This is supposed to conduct lymph. NEAVE points out that the radii are open groves, and on this account not fit for conducting liquids. The fine network he believes to have arisen as the result of careless handling of the scale. He has at all events been able in this way to obtain the formation of fine cracks.

NEAVE's interpretation appears correct. On treatment of entire scales with xylol the fibrillary plate shrinks, giving rise to heavy strains with ensuing formation of cracks both in the fibre plate and in the osseous layer. Local bursts in the fibrillary plate often give occasion to the formation of cracks in the osseous layer directly overhead (Plate 21). The cracks run as a rule more or less perpendicular to the striae, but form a dense network in the troughs. The occurrence of stretches with parallel cracks is of interest. In the neighbourhood of fast-growing corners of the scale the cracks turn away from the corners. In these cases the orientating factor ought to be found in a special arrangement of the fibres in the osseous layer.

The Relation Between the Radii and the Movability of Different Parts of the Body in the Fish

Together with the striae the radii are the most conspicuous morphological elements upon the scales of fishes. For this reason it is natural that their structure and function have been the objects of speculation already while

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Plate 23. Central part of a regenerated scale. STOELTZNER. In the right half of the picture regenerate which has ceased to grow at an early stage, in the left half sectors which continue in outward direction to the periphery. Note the circular striae in these sectors. × 150.

Plate 24. Regenerate with vigorous growth in one direction (arrow). STOELTZNER. Note also striae close to, and parallel with, radii. × 140.

Plate 25. Scales, prevented from growing by the cleithrum. STOELTZNER. × 90.

the first investigations were going on. Thus AGASSIZ (1840),[1] MANDL (1840),[1] and SALBEY (1849)[1] took them for transporting canals. WILLIAMSON (1849)[1] suspected that they were only interruptions of the osseous layer without any special function, while BAUDELOT (1873)[1] assumed that they are formed as the result of irregular calcification.

TAYLOR (1914) considered himself entitled to the statement that the radii function as "hinges" in the scales, and that they permit the scale to adapt its shape in occordance with the movements of the fish. He bases himself, *inter alia,* upon the fact that the number of the radii increases from the head to the caudal axis, i.e. that it is adapted to the differing flexibility of the different parts of the body. With her assertion that the radii function as lymphatic vessels PEVSNER (1926) resumes earlier opinions. The lateral canals described by her are, however, dispatched by NEAVE as cracks caused by careless handling (cf. p. 419). Since the radii are open grooves, NEAVE considers them unfit as canals. He supports instead TAYLOR by demonstrating that also the fibrillary plate is flexible below the radii (cf. p. 401). DIETRICH (1953) supposes that cells move along the radii in a peripheral direction towards the edge of the scale, considering this function more important than their rôle as "hinges".

Material and methods. The investigation was carried out on the scales of roaches. The fishes were separated into three size groups with the length of about 8, 12, and 20 cm, respectively. Each fish was divided into zones according to Fig. 2. Scales were removed in continuous rows in the neighbourhood of the lateral line, where the body of the fish is most flexible. Isolated samples were taken also from other rows of scales, as upon the back and in transverse rows from different parts of the body.

Four types of radii have been distinguished: 1) complete radii, (i.e. radii running uninterruptedly from the focus to the periphery) which reach the edge of the scale within the exposed part of the scale (R_{fe}); 2) incomplete radii (i.e. radii which do not start in the focus or which are interrupted) reaching the edge of the scale within the same part (R_{oe}); 3) complete radii within the unexposed part of the scale (R_{fi}); and 4) incomplete radii from the same region (R_{oi}). A graphical representation has been given of the number of radii of every type upon every scale. The curves in Fig. 3 have been obtained by adding up the radii within each zone.

On scales from which mineral substances and mucopolysaccharides had been removed (method according to RUTH 1946, 1947) the outermost parts of the radii in the periphery have been examined in polarized light.

Observations and discussion. In polarized light collagen fibres can be seen on either side of the radius where it opens into the osseoid rim, whereas it is optically empty right to the periphery (Plate 18). Thus the radius differs from

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[1] Quoted after TAYLOR (1914).

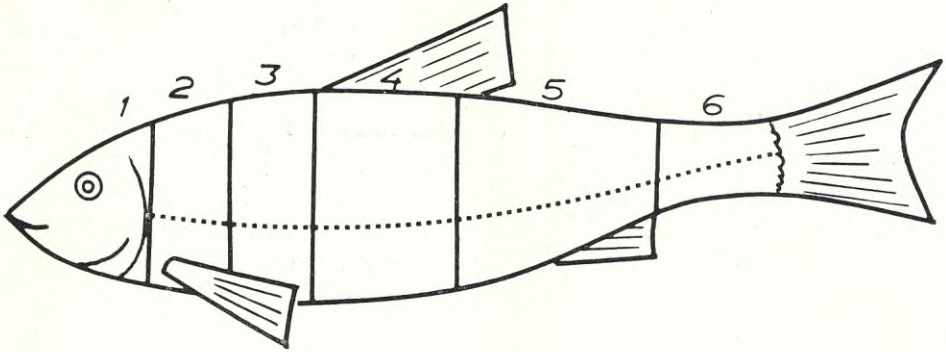


Fig. 2. Division of the roach into zones for the counting of the radii.

its surroundings already at the time when the collagenous matrix is preformed. The process of calcification is without importance for the formation of radii. Radii are occasionally formed from an edge of erosion at regeneration after the disintegration of a scale. These issue frequently from the edge of erosion, and remain then as permanent features in the scale. In this case they ought to have been formed in the same way as that described for normal regeneration, i.e. they ought to constitute the boundaries between different groups of cells which form the osseous layer.

It is typical for the scale of the roach that a radius, once formed, continues to diverge from the surrounding osseoid zone in the periphery of the scale. Radii which end blindly within the osseous layer have been observed only in a few cases. On this account the numbers of complete radii in fishes of different size ought to be directly comparable. The incomplete radii, however, which can be formed at any time in the life of the fish, can consequently occur in different numbers, depending on new circumstances initiating the formation of radii.

The number of the complete radii upon the exposed part of the scale (R_{fe}) increases inconsiderably from the head of the fish to zone 5 (Fig. 3: r). Upon the caudal axis it reaches a noticeably higher value. The course of the curves for the incomplete radii from the exposed part (R_{oe}) is on the whole the opposite of that of the curves for R_{fe}. The averages for the numbers of radii from one and the same zone differ with 1—2 between different fishes. Also the curve for R_{fi} exhibits a strong increase from the head to the caudal axis. Here the variation between different fishes is greater, amounting to up to four radii.

In contradistinction to the above mentioned radii the group R_{oi} exhibits a distinct dependence on the size of the fish. In the smaller animals (about 8 cm) the curve is rather irregular, but has a clear rise at zone 6. The variation of the averages from one fish to the other amounts to about 3 radii. Within the 12 cm-group the curves exhibit a steep rise to zone 5, reaching values higher than those for R_{fi} in the same zone. This maximum is followed by a drop to zone 6. The variation between different fishes amounts to eight radii. Curves for fishes within the 20 cm-group or larger show the same steep rise to zone 5. The variation within this group amounts to at most six radii.

From the above observations it is obvious that the number of complete radii of the entire scale rises from the head towards the caudal axis. A remarkably high value is obtained exactly for the very flexible caudal axis. This gives additional support to TAYLOR's hypothesis. The number of complete radii is on the other hand larger upon the dorsal side in spite of the fact that here smaller demands are made upon the flexibility of the scales. If the total number of radii from the exposed parts of the scales is taken into account, it is found to be rather constant with the exception of zone 6, where it is higher than elsewhere. Also this supports to some extent TAYLOR's conception. It can, however, not be disregarded that the flexibility is much greater in zone 5 than in the zones 1 and 2.

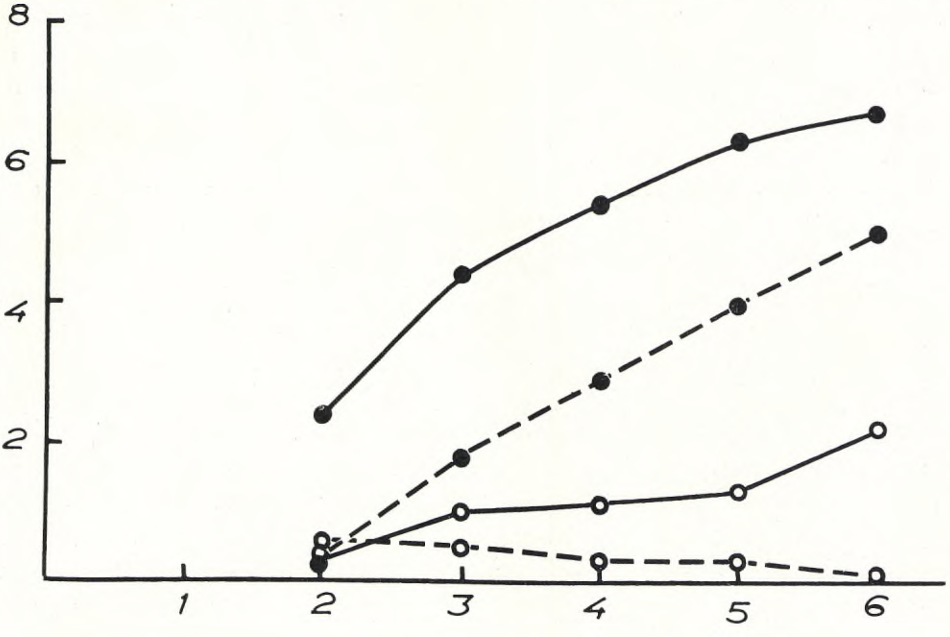
The scale is, however, obviously subject to certain influences which cause the formation of the radii. If radii have not been formed in sufficient number from the focus, incomplete radii appear later as new formations. This might perhaps explain why the curves show a more or less inverted course with respect to each other.

As can be seen in Fig. 3 incomplete radii are developed in fishes of about 9—10 cm length within the unexposed part of the scales, obviously at a fast rate. These radii account for the distinct maximum for zone 5. This seems to be connected with the fact that within this zone the scales possess in their cranial edge several deep notches, separated by faster growing extensions. Centripetally the radii end near a line which can be drawn from the focus to the extreme end of the extension, i.e. these radii are formed where the growth of the scale is particularly fast in respect to that of the surrounding parts (Plate 22).

Fig. 3. The radii of the scale of the roach. Ordinata: Number of radii per scale (average), abscissa: the zones of the fish (see fig. 2).

●——— Complete radii from the unexposed part of the scale.
●- —— Incomplete radii from the unexposed part of the scale.
○——— Complete radii from the exposed part of the scale.
○- —— Incomplete radii from the exposed part of the scale.

a = specimen 1, 8 cm of length; b = specimen 2, 7.5 cm; c = specimen 3, 8 cm; d = specimen 4, 8 cm; e = specimen 5, 13.5 cm; f = specimen 6, 12 cm; g = specimen 7, 15 cm; first row above the lateral line; h = same specimen, first row below the lateral line; i = specimen 8, 12 cm; k = specimen 9, 12 cm; l = specimen 10, 12 cm, scales from the back; m = specimen 11, 24 cm; o = specimen 12, 19 cm; p = specimen 13, 18 cm; r = the complete radii from the scale of the roach.



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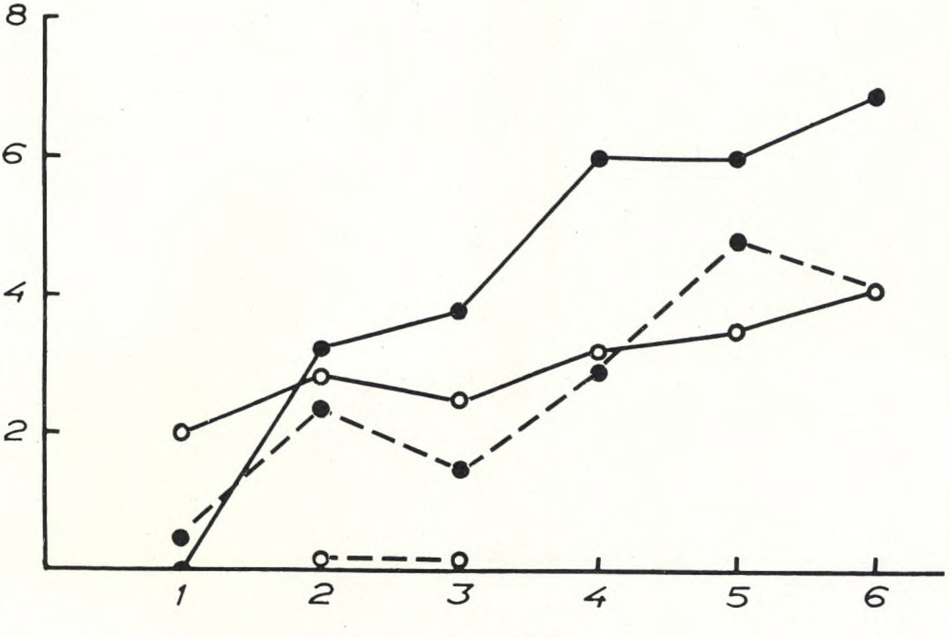

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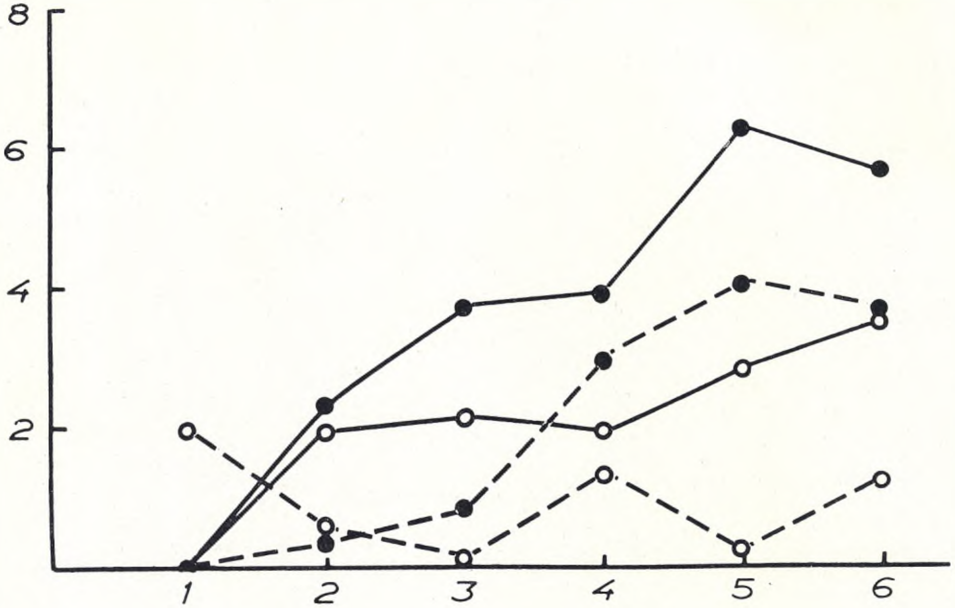

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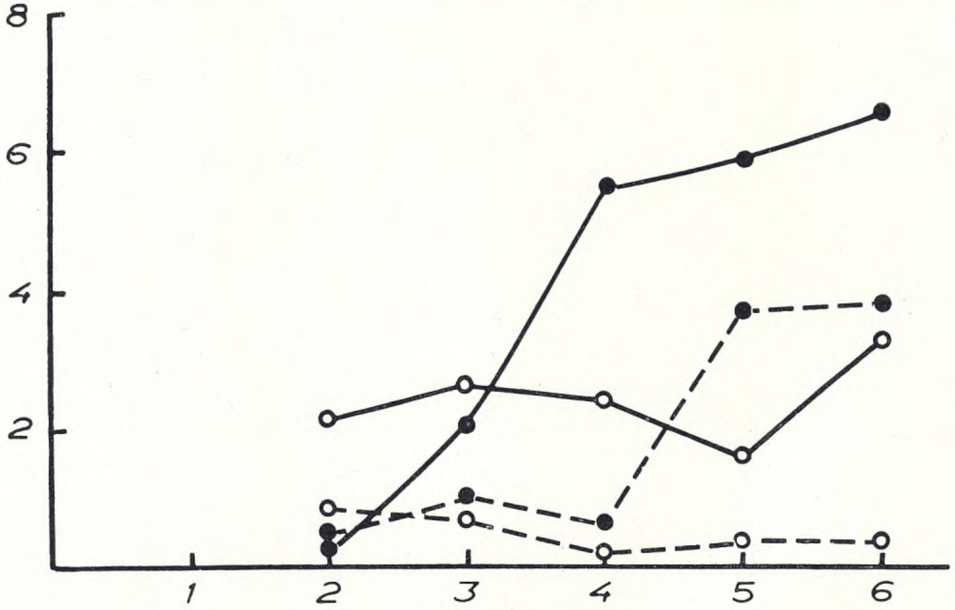

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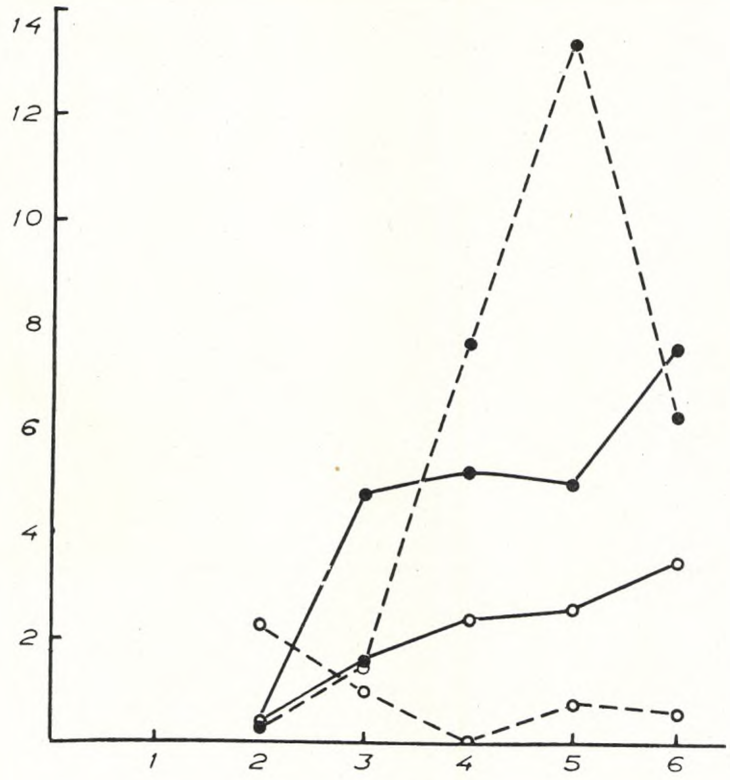

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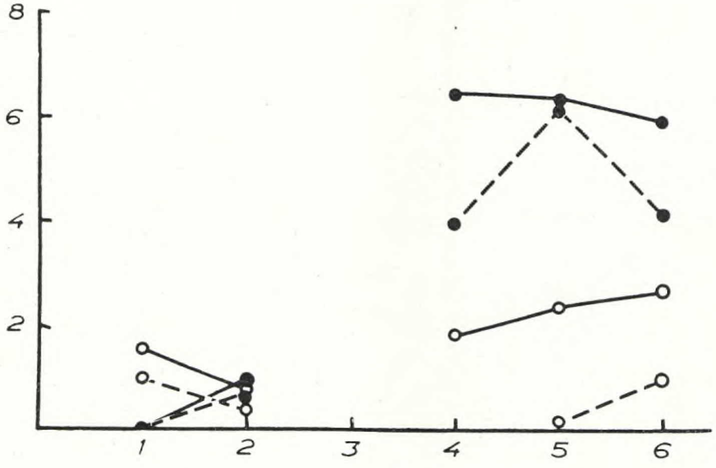

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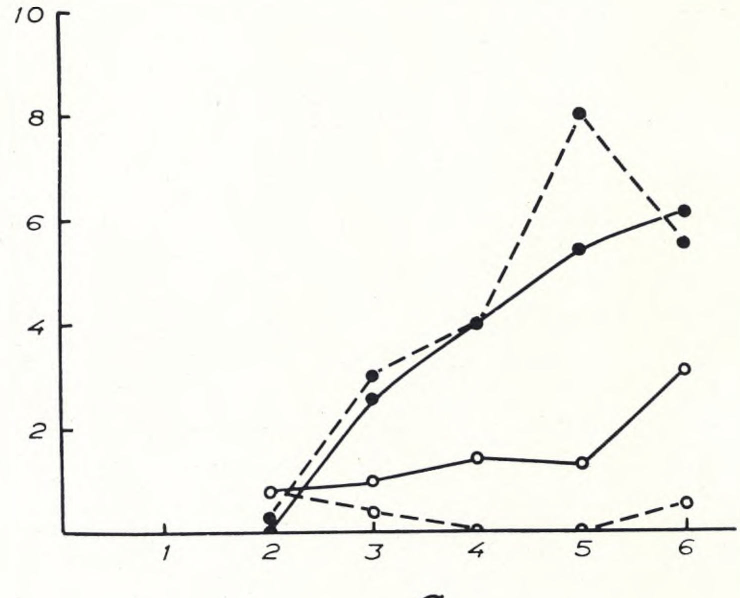

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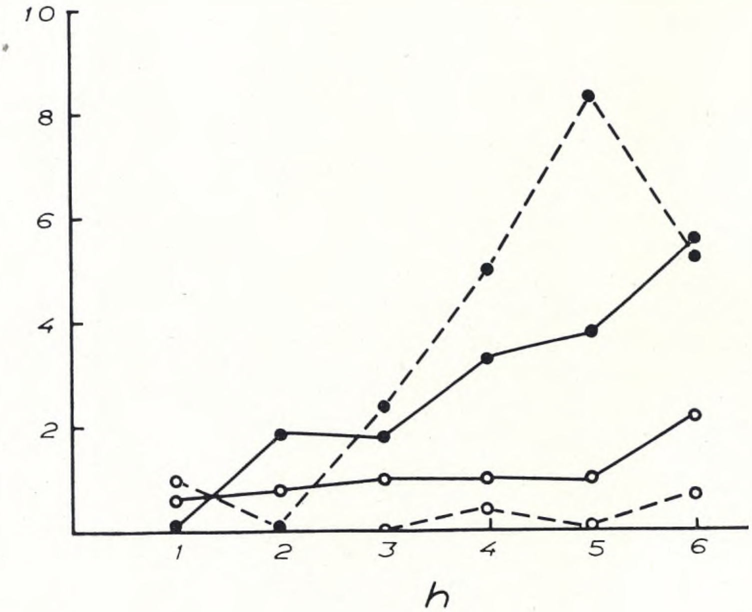

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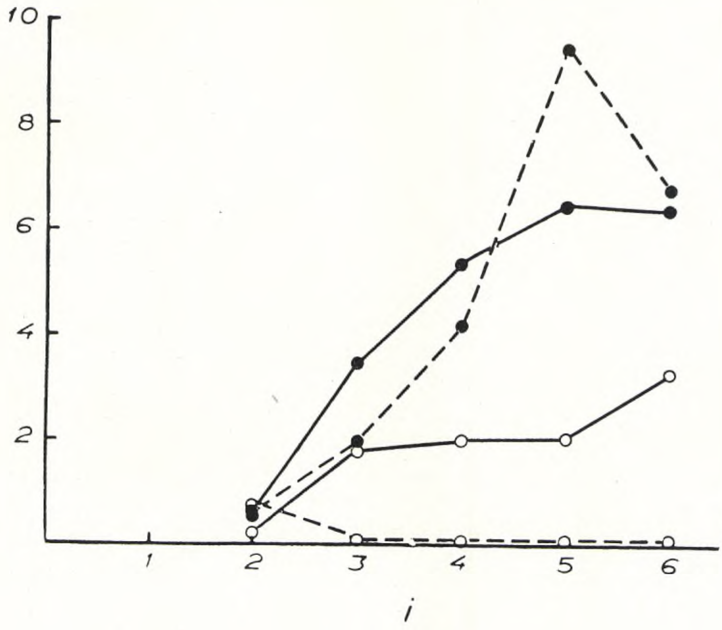
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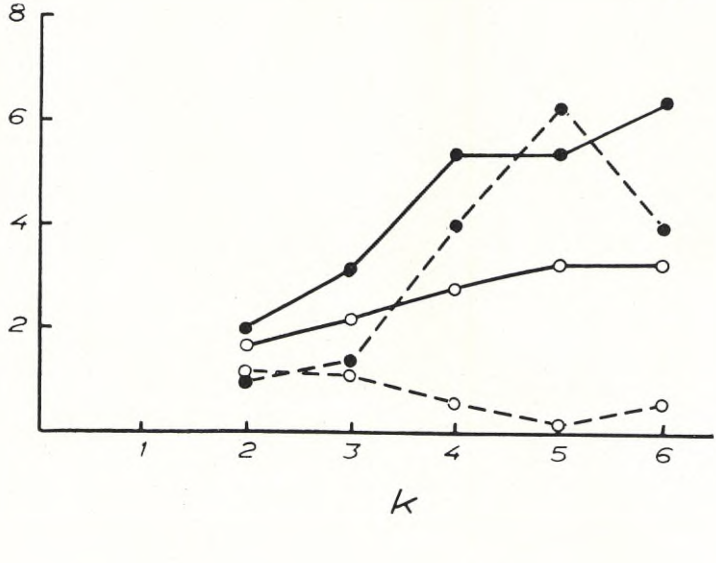
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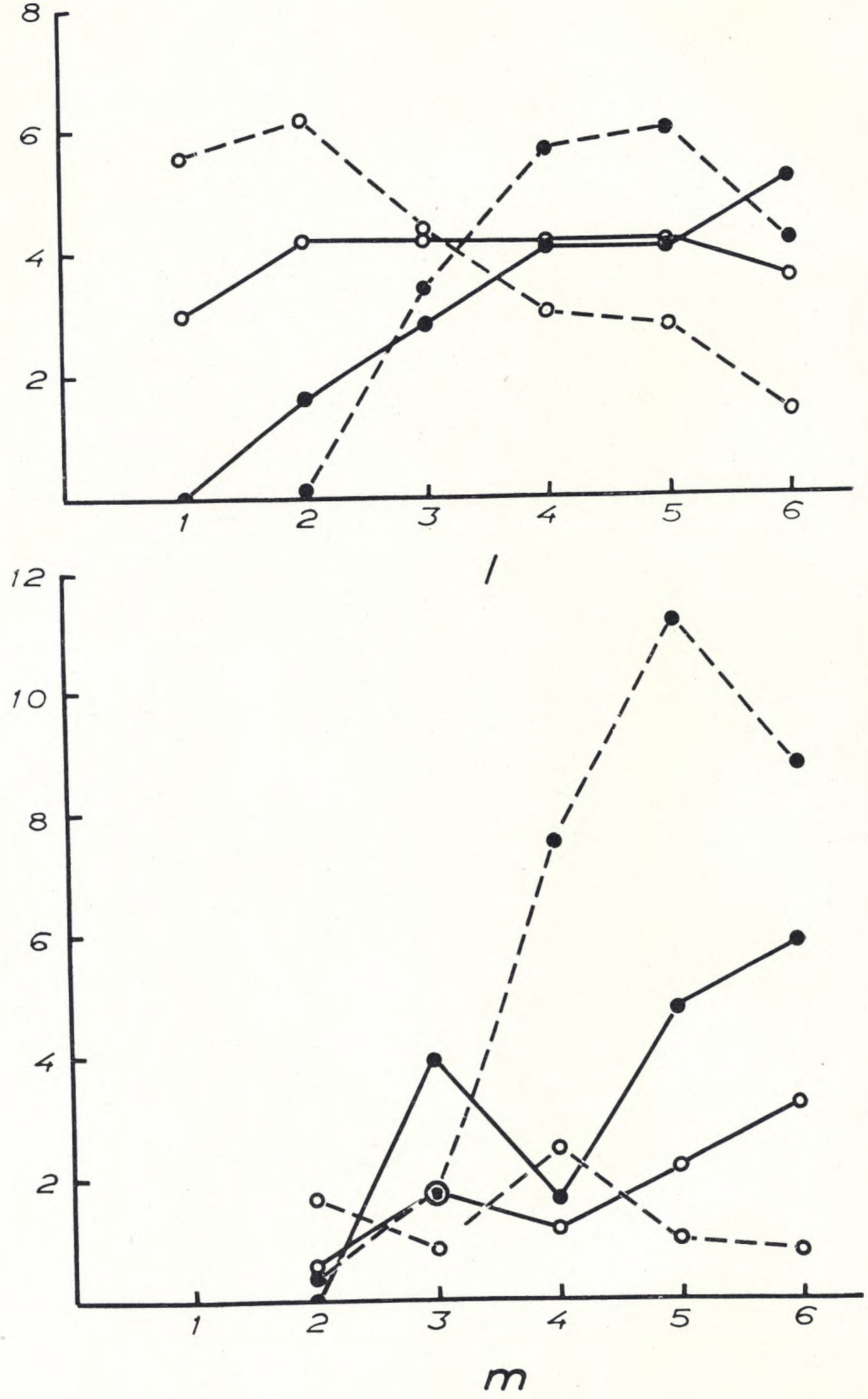
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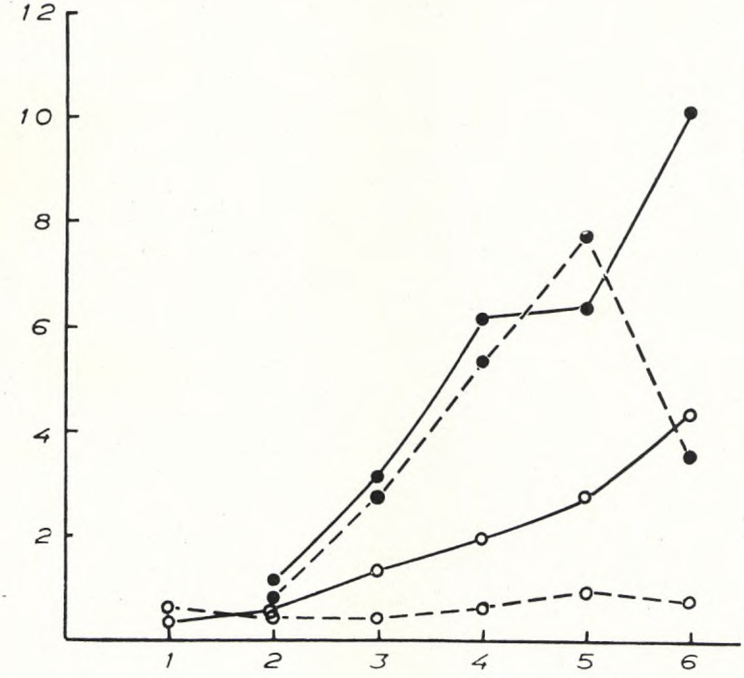

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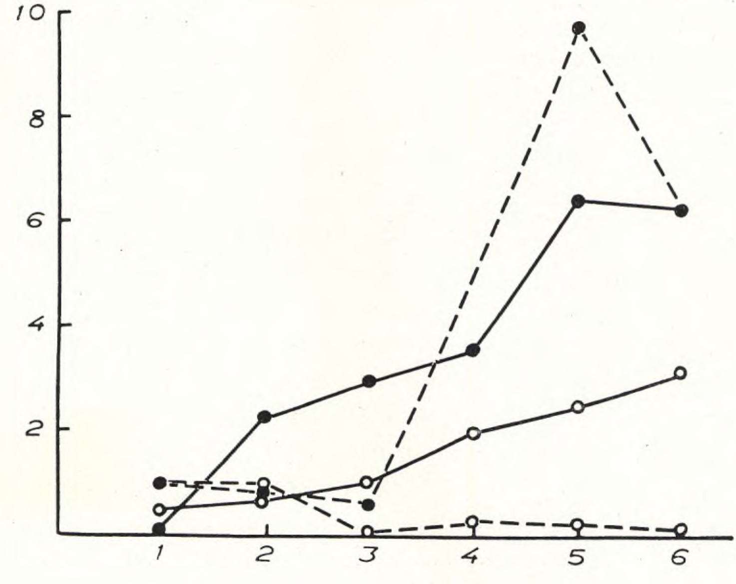

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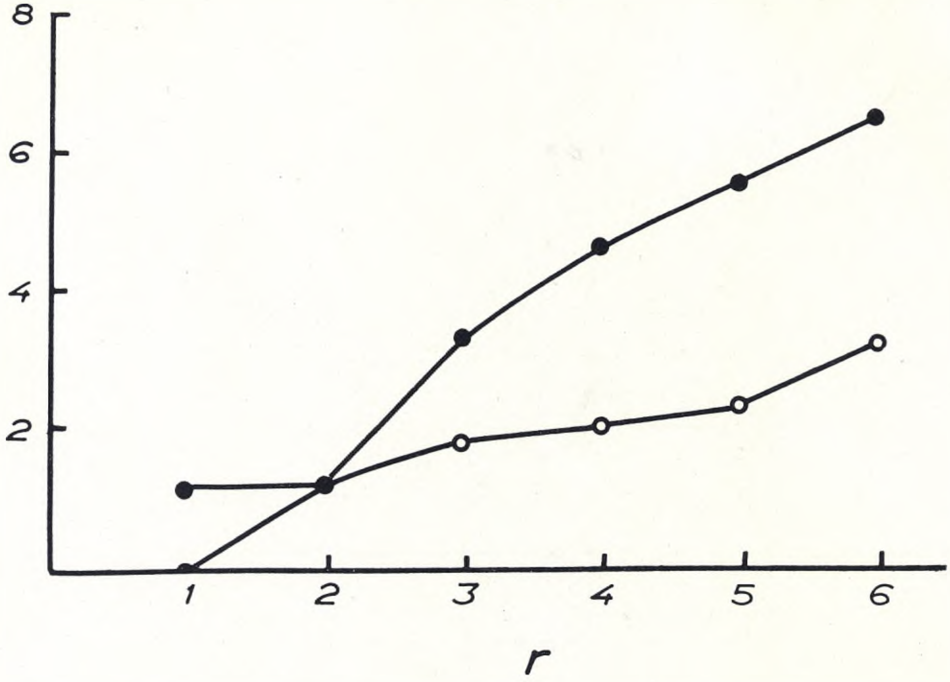


The results of this partial examination neither prove nor entirely refute TAYLOR's hypothesis that the radii render the scales flexible. It is, however, difficult to understand in what way the majority of the radii should be able to fulfill this function, as they include only a small angle with the longitudinal axis of the scale. If they were arranged at right angles to the longitudinal axis the efficiency would be much greater.

As things are only two radii would be fit to act as "hinges", viz. the complete radii which reach the edge of the scale at the boundary between the exposed and the unexposed part of the scale (Fig. 4). One of these radii is parallel, the other perpendicular to the myomeres. They thus coincide with the muscle septa, and are on this account fit for adaptating themselves to the contractions and extensions of the myomeres. These radii form long "lines of bending", as can be seen in Fig. 4. This coincidence with the muscle septa occurs also in cases where the scale has developed obliquely in the scale pocket. Then the radii are displaced in such a way as to fit into the lines of bending. The observation has also been made that the radii in question occur less often upon the back of the fish. This supports the assumption that they are of importance for the flexibility of the scale, since this type of bending does not occur upon the dorsal side.

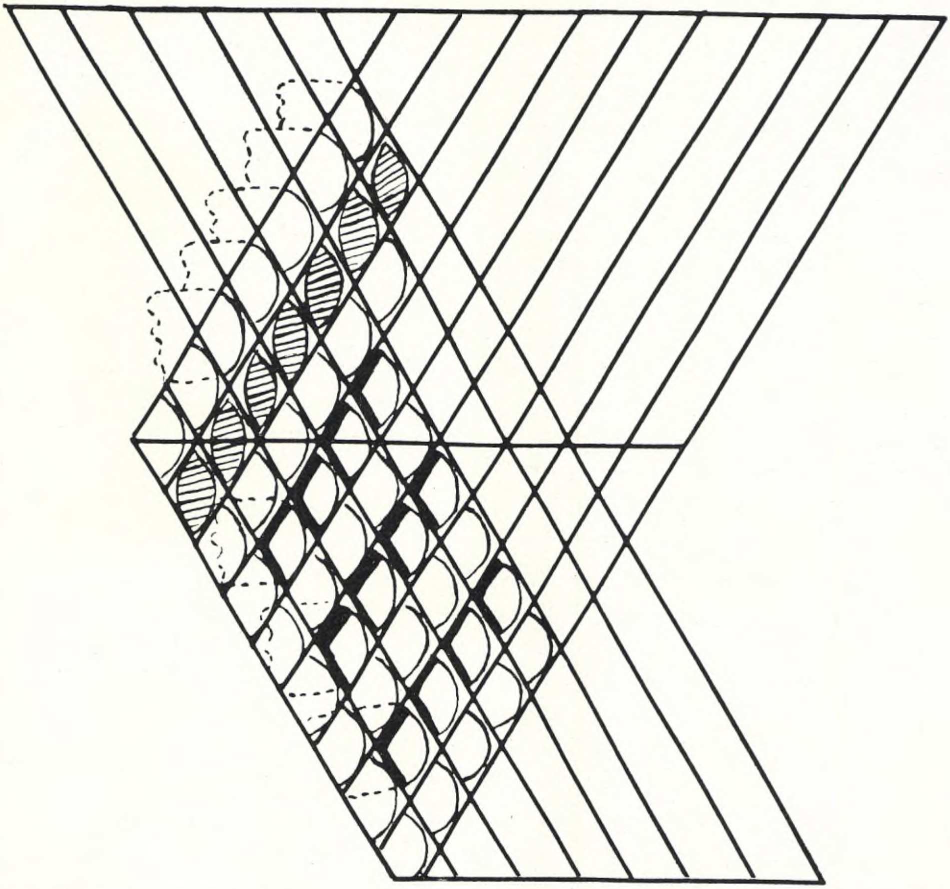


Fig. 4. Diagram for the position of the scales and of the myomeres in the roach. Hatched = exposed part of the scale. Dense black has been used for the radii which by the coincidence of the series of scales with the metameres form "bending lines".

The Induction and Formation of the Striae

Introduction. Since Hoffbauer (1899) had demonstrated the possibility of determining the age of fishes by means of "scale reading" the scales have been studied mainly with regard to their formation and histology. As the determinations of age are based upon the arrangement of the striae and their distance from each other, the origin of the striae has attracted special interest. During periods of fast growth, e.g. in summer, the striae are formed with greater mutual distances, and form a "summer ring". Slower growth is registered by a so called "winter ring" with closely set or incomplete striae.

Exposition of the problem. In earlier examinations hypotheses on the course of the induction, origin, and development of the stria have been based upon observations of the arrangement of cells and striae on generally stained histological preparations. No experiments had earlier been made in an attempt to influence the formation of striae. These older hypotheses contradict each other, and do not elucidate the problems of the formation of the striae. For this reason it is necessary to attack them afresh, experimentally and with modern methods. Summarily the problems can be arranged in four groups: 1) induction of the individual stria, 2) origin and development of the stria, 3) course of the stria, and 4) height of the stria.

Material and methods. For the study of the formation of the striae mainly sections through the skin of roaches and preparations of entire scales of roach have been used. These were in most cases fixed in absolute alcohol. The sections were 7—10 μ thick. For general purposes they were stained with Heidenhain's Azan and with haematoxylin-eosin, for the demonstration of metachromatic substances with toluidine blue, and of nucleic acids with methyl green-pyronine. The calcification was traced by means of the methods according to STOELTZNER and v. KOSSA.

The most important results have been obtained by the study of whole mounts. In these the nuclei of the cells have been stained with gallocyanine--chrome alum, with haematoxylin, and with iodine-potassium iodide. The reagents for nucleic acids and the salts of calcium are the same as those used on the thin sections. The boundaries of the cells have been determined in unfixed scales by means of silver nitrate and STOELTZNER's method. On account of their small thickness also entirely untreated scales are fit for examination under the phase-contrast microscope. The elevation of the striae over the troughs belonging to them has been studied with the aid of the stereo attachment (see p. 391).

Experiments and observations. 1) The induction of the individual stria. The stria originates under a fold of protein-forming cells. This process will be dealt with in detail below (see p. 438). Earlier authors have discussed the preceding induction of the stria in a rather superficial way. NEAVE, however, observes that a local obstacle to the growth of the scale causes high and closely set striae. On account of unsuitable methods and the incomplete information about the formation of the collagen at that time NEAVE was not able fully to utilize his observations.

On account of preliminary observations the present investigation was based upon the working hypothesis that the formation of striae is induced by an external resistance to the spreading of the scale. In the following section the writer will account for experimental results and for observations on normally growing scales which support this hypothesis.

In a series of experiments a thin rubber-sheet was streched round the middle of a fish with the intention of studying the influence of the pressure caused by the rubber-sheet upon the formation of striae upon the scales involved. The duration of the experiments was, however, short as it was not possible to attach the rubber-sheet without, in the long run, injuring the fish. On this account these experiments have for the time being to be regarded as failures.

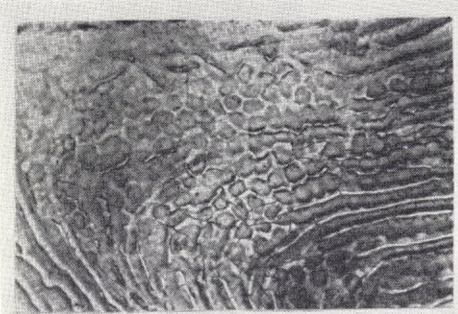
Certain features in the development of the regenerating scales indicate that both a regeneration taking its normal course and one which is experimentally influenced might be able to give valuable informations about the induction of the striae.

A regenerated scale differs from a normal one by the lack of the focus, its central portion being occupied by more or less rounded isolated plates of the osseous layer which are separated from each other by furrows resembling radii. The plates of bone originate about simultaneously, and grow in all directions. When they meet, growth ceases. Only the peripheral plates are able to continue to grow and to form larger portions of the osseous layer. The edges of a bone plate are often situated slightly above or below those of adjacent plates. The mutual resistance and the pressure they exert upon one another before growth comes to a standstill evidently forces the edges out of their normal direction of growth, parallel with the surface of the skin.

The central parts of the above described plates are as a rule without striae of normal type. These parts are occupied by a network of haphazardly arranged ridges which are lower than striae, and sometimes lack the sharp "edge" characteristic for them. The ridges enclose groups of cells forming uniform "centres of activity". The first stria appears only in the periphery. For this reason a plate in the central part of the scale usually has at the periphery a stria which runs roughly parallel with the edge. A sector-shaped plate, on the other hand, with possibility of unlimited growth at least in one direction possesses at the apex of the sector one or several striae which run towards the centre of the scale (Plate 23). These are followed by some irregular ridges which are gradually transformed into normal striae. These are directed towards the edge of the scale.

The arrangement of the striae in the regenerated scale indicates that the pressure exerted between the plates of the scale, and which forces their edges above or below each other induces also the formation of the striae. The following experiments and observations supply additional support for the hypothesis mentioned in the introduction to the effect that, as the result of a resistance in the direction of the growth of the scale, a fold should be formed in the assemblage of cells which forms the striae.

Within an area of about 4 cm^2 upon the side of the fish the scales were removed with the exception of some which were regularly distributed over the entire surface, and consequently situated at certain distances from each other. During the subsequent regeneration new scales were developed around these left-over scales and at the margin of the surface of regeneration. These new scales were prevented from growing in certain directions, but had complete freedom to develop in others. The parts of the newly formed scales



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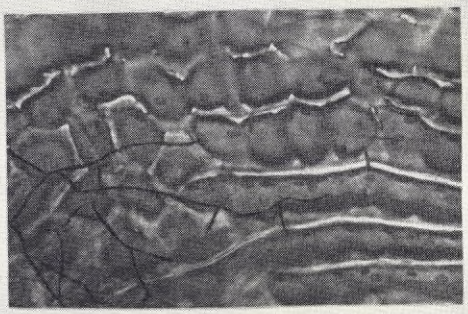

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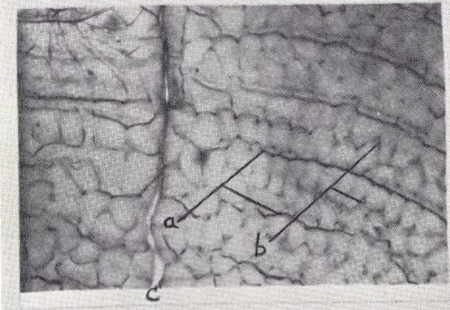

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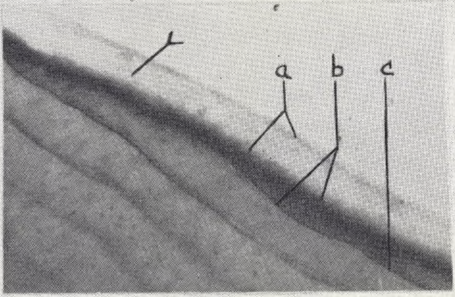

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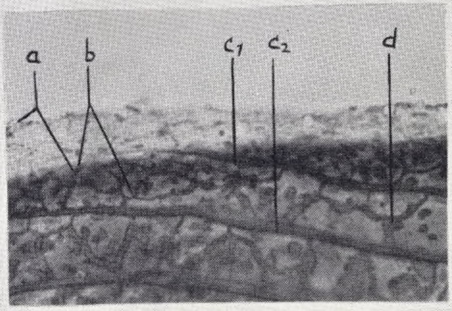

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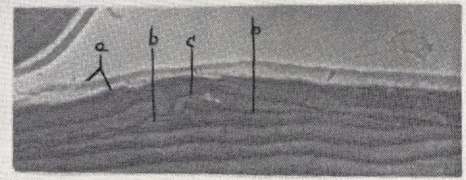

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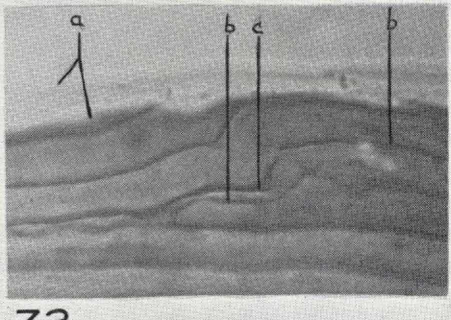

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Plate 26. Modification of the morphology of the stria at locally increased growth. Stoeltzner. Growth of the scale most vigorous in the direction towards the left upper corner of the picture. × 230.

Plate 27. Part enlargement of the preceding picture. × 580.

which early in their growth met with a resistance developed striae at the time in question. Parts of scales, on the other hand, which grew without hindrance lacked striae over the greater part of their surface (Plate 24). Striae were formed only in the periphery, when the scales approached their original size.

The result of an extremely vigorous resistance against the growth of the scale can be seen in a number of normal scales from the border of the gill opening (Plate 25). Here a bone, the cleithrum, prevents the development of the cranial portion of the scale. This is strongly reduced with closely set, high striae with well developed "teeth".

Thus support for the theory of the induction of the formation of the striae by a resistance to the growth of the scale can be adduced both from regenerated and from normal scales. Also the result of the absence of resistance, when no striae are formed can often be studied upon regenerated scales .(see above). In normal scales the corresponding phenomenon is less easily observed. Below an account will be given of a case of local increase of surface in an aberrant scale the shape of which can be supposed to be connected with an absence of resistance to the spreading of the scale.

The Plates 26—27 represent a strongly developed "corner" of an otherwise normal scale. The assumption ought to be permissible that the great increase of surface of the "corner" depends on the local absence of a normally occurring counter-pressure which would limit surface growth. If we here follow the normal striae towards the "corner" we find a gradual transition into irregular ridges. The straight crest of the stria breaks up, and is replaced by polygonal to rounded elevations which enclose bowl-shaped depressions with one or a couple of nuclei at the bottom. These latter are most probably remains of the scale-forming cells, and the borders of the "bowls" are limited by the "areas of activity". Only indications of unevenness on the part of the surface of the osseous layer are found within the portion, where the increase of surface has been greatest. When the influence of the factor inducing striae diminishes, the increase of surface is made possible. The material which

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Plate 28. Normal and "accessory" striae at fast growth of the scale. STOELTZNER. a = normal striae, b = "accessory" striae, c = radius. × 390.

Plate 29. Passage of the stria through the zone of calcification. STOELTZNER. a = osseoid zone, b = zone of calcification, c = stria. The arrow indicates the outermost part of the striae under formation in the osseoid zone. × 550.

Plate 30. Boundaries of cells in the periphery of the scale. STOELTZNER. a = osseoid zone, b = zone of calcification, c_1 = the outermost stria, c_2 = the outermost but one stria, d = boundaries of cells. × 600.

Plate 31. Regeneration with formation of striae after resorption. STOLTZNER. a = osseoid zone, b = limit of resorption, edge of erosion, c = the first-formed stria. × 190.

Plate 32. Part enlargement of the preceding picture. For the signs, see Plate 31. × 560.

normally should have entered into the formation of the striae seems now to be consumed in the increase of surface.

The morphology of the striae changes within one and the same scale. Schematical representations of the two extremes are given in Fig. 5. Common to the different types is a more or less steeply inclined slope towards the crest of the scale. The slope of the surface which faces the centre of the scale is considerably steeper. Here the crest of the stria often forms an overhang.

The shapes of the striae permit correlation with the rate of growth. In the exposed parts of the scale, where the increase of surface is rapid, the striae are low with a feeble slope towards the edge of the scale and a great distance between their crests. The cranial part of the scale with its slower increase of surface is covered by high, steep, and closely set striae.

The assumption lies most closely at hand that the dermis, being denser at the bottom and the sides of the scale pocket, offers to the growth of the scale a resistance which is approximately proportionate to the density of the tissue. This assumption is supported by the fact that the boundary between the unexposed and the exposed parts of a normal scale is very distinct with regard to the configuration of the striae. This boundary is, furthermore, absent in a scale of which no part is situated in a scale pocket. The striae follow a practically circular course, and their mutual distance is the same all around the scale.

Scales of the herring differ distinctly from those of the roach. The exposed part is entirely without striae, the part which is hidden in the scale pocket exhibiting striae which run roughly transversally across the scale. Scales of this type occur upon the lateral sides of the herring, where the dermis is very thin, and where the scales easily loosen from the pockets. The scales upon the dorsal side resemble, however, the scales of the roach. Between back and sides these two types of scales pass continuously into another (SAVAGE 1919). It is an interesting fact that upon the dorsal side the dermis is much thicker, and that there the scales are solidly attached in the pockets. Thus we find in the herring an obvious connection between the morphology of the scales and the density and thickness of the dermis.

In this connection the following case is of great interest. From a brown-trout MÜLLER (1953) has described a scale of Clupeid type. This information proves the lability of the circumstances which influence the course of the striae. In accordance with the first way of reasoning the thickness of the skin must be assumed to have been considerably below normal in the place where the described scale has been formed, but the author makes no statement pointing in this direction.

Apart from the dermis also other factors are active in the normal induction of striae. NEAVE demonstrated the mistake in the assumption that in a regenerating scale striae are formed only when the scale has completely filled

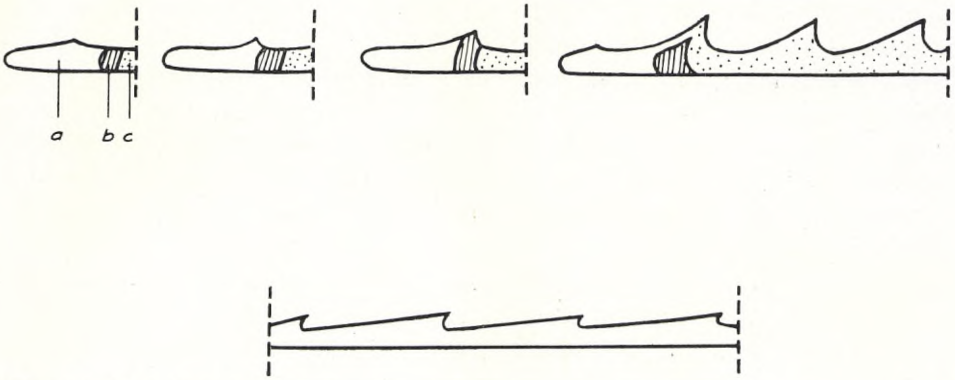

Fig. 5. Diagram illustrating the formation of striae, and typical striae from the unexposed (the upper pictures) and from the exposed part (the lower pictures) of the scale, respectively. a = osseoid zone; b = calcification zone; c = calcified scale.

the scale pocket, i.e. has attained the size of the original scale. Since striae are formed before the regenerate has reached contact with the walls of the pocket, a factor must function here resembling in a way the influence of the dermis. This applies also to the limited regeneration after resorbtion of the edge of the scale. It is possible that also the fusiform inactive cells in the periphery of the scale, which seem to be in a very solid arrangement, oppose the expansion of the scale, and induce striae in the regenerating scale.

The scale shown in Plate 20 exhibits a seldom occurring irregularity in the formation of the striae. This scale, like all in the roach in question, has between the sparsely set striae of the caudal part a zone of irregular ridges (a), while the cranial part shows closely set and high striae (b). The "bowl-shaped depressions" agree in their appearance with those occurring in regenerating scales prior to the appearance of normal striae. As a vague suggestion only it might be proposed that in this fish the dermis and with it the connection between the inactive cells in the periphery of the scale have been so loose that the normal "damming up" of the growth of the scale has not taken place. Normal striae are formed only when the epidermis or the denser dermis in the scale pocket forms a greater obstacle to the spreading of the scale.

According to an earlier conception the striae should be formed by a calcified boundary between cells. The erroneousness of this assumption can be demonstrated with the help of Plate 28. This picture represents a regenerating scale in which the formation of normal striae has begun. They are low and irregular, and set at great distance from each other. Between each pair of striae a very low and irregular ridge is found. This ought to be a calcification of the boundary between cells, described on p. 438.

2) Origin and development of the stria. In the foregoing it

has been reported that in several earlier investigations the cells had been considered to determine the course of the stria in different ways. Also this investigations started from the working hypothesis that the stria should be formed between two rows of cells. This opinion was, however, not supported by the staining of nuclei and cell boundaries. It could, on the contrary, be seen that a fold is formed in a whole assemblage of scaleforming cells, and that an insignificant thickening of the osseoid is formed in this fold. In connection with the calcification new material is added to this thickening which grows out into a complete stria. Below an account is given of the whole course of the origin and development of a stria upon a normal scale.

Under the phase-contrast microscope combined with the stereo attachement the extreme portion of a freely ending stria can be seen in whole mounts in the osseoid zone, as a rule roughly in the middle of it (Plate 29). This presumptive stria is a low and narrow rise upon the otherwise smooth surface. In the direction towards the zone of calcification the stria reaches a height of about 3—4 μ. Within the zone of calcification the height of the stria increases rapidly. When ready formed it is about 12—15 μ high. (These values have been read on the fine adjustment screw of the microscope, and agree on the whole with the results of measurements taken on pictures obtained by electron microscopy; SIGNER, v. BEUST, and CORTI 1951).

The greatest interest is linked to the point, where the stria first rises above the osseoid. There one or several factors have changed in relation to the part of the osseoid zone without striae. These cause the origin of the stria. The study of the arrangement of the cells is, however, made difficult by the fact that the boundaries of the cells across the osseoid zone cannot be stained with the above-mentioned methods. This is probably due to the circumstance that the substance in the walls of the cells to which the metal ions are adsorbed is not developed before the cells have been in a state of activity for some time. The positions of the nuclei do, however, not point to any special arrangement of the cells. These seem to be arranged irregularly along the germ of the stria and in its prolongation upon the smooth osseoid surface.

Roughly at the outer border of the zone of calcification the staining of the boundaries of the cells becomes possible. A network of boundaries of cells, apparently without regular arrangement, is found upon that face of the stria which is directed towards the periphery. Where this stria turns to become the outermost but one, and where it is thus separated by one stria from the edge of the scale, the irregular boundaries of the cells are as a rule replaced by one boundary (occasionally by two, rarely more, Plate 30). This runs fairly parallel with the striae and roughly in the middle of the trough. Within the completely calcified part of the scale also this boundary disappears, and in the central portions only the boundaries of the cells across the troughs are left.

The connection between the stria and the cells that form it is seen best at the transition between the zone of calcification and the osseoid zone. Under favourable conditions both the uncalcified and the calcified part of the stria as well as the superimposed cells can be distinguished simultaneously. The boundary between the bone stained brown by STOELTZNER's reaction and the thin overlying osseoid layer is distinct. Above, and in the continuation of the latter an indication of a fold is seen in the whole assemblage of cells. On account of the size of the active cells and of the wealth of plasm the fold is often distinct under lower magnifications as an optically denser layer.

The fast increase in height of the stria during calcification indicates that this process is of vital importance for its formation. A study of thin sections through the edge of the scale confirms this. Staining with toluidine blue has given the clearest results.

Also in sections the osseoid stria can be seen as an insignificant elevation. During the approach of the zone of calcification it increases somewhat in height. The calcification begins at the base of the stria, and spreads upwards in it. The scale-forming cells deposit newly formed proteins upon the hardening stria (Plate 4). The proteins "ripen", become calcified, and are covered by new material as long as the cells remain active.

3) The course of the stria. Both the building-up of a new osseous layer and certain features in the formation of a stria can be studied during the regeneration of the scale which follows upon its resorbtion caused by lack of vitamin D, after the experimental diet has been replaced by adequate food (Cf. pp. 413 ff.). When osseoid was formed, it was covered by cells with large nuclei and rich in plasm which were of the type described in the normal formation of scales. The germ of the first stria was formed, while the osseoid zone was still narrow, and before calcification had taken place. The course of the stria agreed closely with that of the edge of erosion (Plates 31—32). The course of the stria was evidently determined by the solid and hard osseous layer on its inner side, while the smooth edge of the osseoid zone remained passive in this respect. The distance between the first stria and the edge of erosion was considerably greater than the distances between the striae upon the normal osseous layer inside the edge. The width of the osseoid increased quickly, and in this connection the distances between the striae grew. The irregularities in the configuration of the edge of erosion which had set their stamp upon the course of the first stria were transmitted also to the following, yet with decreasing effect. The stria which follows the edge of erosion now obviously performs the function of the solid and hard osseous layer. During the earlier stage of the regeneration the zone of calcification was broad, but its width decreased to about the same extent as that of the osseoid, when the scale was about to reach its original shape.

4) The height of the stria. Height and shape of the striae vary within wide limits even within one and the same scale (cf. p. 435). In the cranial part of the scale, which is sunk into the scale pocket, the striae are

high and "wave-shaped». The distances between the striae are short. Upon the caudal, exposed part of the scale the striae are lower and more distant from each other. It is characteristic that the distances between a series of striae, e.g. in a section, are very constant with exception of the transitions between "summer rings and winter rings". The quantity of material which enters into the formation of a stria is as a rule larger than that of the intervening trough. For this reason it seems probable that the cells which produce the stria remain active during a longer period than those below the trough. Alternatively the assumption is of course possible that the cells forming the stria produce a greater amount of scale material per unit of time. In this case this might depend on an excitation of the active cells by the pressure exerted by the growing stria.

Summary. On the base of the reported observations a new hypothesis can be advanced for the formation of the striae: At the transformation of the cells an obstacle in the direction of the growth of the scale (dermis, inactive preparatory stage of the scale-forming cells, or another factor) causes in the assemblage of cells a pressure between the obstacle in question and the calcified scale on the inside. Periodically, on reaching a threshold value, this pressure induces the formation of a fold which temporarily removes the pressure.

The osseoid is deposited in the trough in the shape of a low ridge. The cells remain active while the calcification of the stria goes on, and for this reason osseoid is successively deposited upon the hardening stria. This thereby increases rapidly in height when the osseoid is calcified, and the deposited material lifts up the active cells (Fig. 1). Once these cells have been transformed into osteocytes, and the stria has become completely calcified, no more material is added to the stria.

In the foregoing two alternatives have been proposed, both implying obstacles to the increase of the surface of the scale, consisting in structures in the immediate vicinity of the edge of the scale. In either case the calcified scale on the inner side or the last fully developed stria function as an immovable barreer. Between this and the outer structure takes place the transformation of active ellipsoidal cells from their elongated fusiform predecessors in the periphery of the scale. At the transformation the cells grow in thickness, and require more space. Resistance from three directions, viz. from outside and inside, and from below, caused by the osseoid forces the cells upwards. The formation of the folds would thus become the result of the accumulated pressure which at regular intervals, i.e. when the pressure has reached a certain theshold value, forces the cells upwards. This increase of the surface of the assemblage of cells temporarily removes the pressure. Afterwards it rises again towards the next critical peak. There remains no doubt that a formation of folds in the assemblage of cells is the base of the normal formation of striae. A deposition of osseoid between rows of cells produces by itself only low and irregular ridges (Plate 28). Also the fundamental importance of the calcification for the growth in height of the stria appears indisputable. The increase in height at calcification is directly measurable, and can be followed in series of sections.

Series of experiments with regeneration of resorbed edges of scales demonstrate the dependence of the configuration of the first newly formed stria upon the edge of erosion behind it. But also later formed striae are influenced, i.e. the course of a stria is determined to a large extent by that of the immediately preceding (Plates 31—32). This is in good agreement with the above discussion. Of a stria forming a bulge towards the periphery this bent part is younger than its other, farther inside situated portions. Thus the cells outside the bulge are upon an earlier stage of their transformation, and the pressure is consequently lower there than in front of the major part of the stria. For this reason the formation of a new stria will take place earlier outside the older part of an existing stria than outside its bulge. This can be observed without difficulty in a number of preparations of entire scales.

The Formation of the "Winter ring" in Relation to the Annual Cycle of the Scale

Introduction. It is a generally accepted older opinion that rapid growth of the fish during the warm season leads to greater intervals between the striae. With a slowing down of growth during autumn and winter, however, the striae are set more closely or are incomplete, and form a "winter ring" or annulus. From later papers, e.g. by SEGERSTRÅLE (1932), BECKMAN (1942), JONES (1953), and TESCH (1955), it is, however, evident that the "winter ring" is on the contrary formed during spring and early summer, i.e. at the beginning of the estival growth. BECKMAN proves with perfect evidence the dependence of the formation of the structure on a certain minimum temperature, but none of the three first-named authors advances any histological points of view. TESCH presumes "that a certain increase of calcified substances takes place without a simultaneous augmentation of the organic substance".[1] This he believes to lead to well developed, but closely set striae. His reasoning is based upon antiquated statements by HASE (1911) which do not agree with our present knowledge about the formation of bone.

In dealing with the regeneration of resorbed edges of scales we have shown in the foregoing that the first-formed striae are often close to each other with a small osseoid zone outside the periphery of the scale, but that the distances between the striae increase at a fast rate, while at the same time the zones of osseoid and of calcification increase in width (see p. 439). This

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[1] Author's translation.

problem has been attacked experimentally with the aim of elucidating the changes of the zone of growth at different temperatures.

Material and methods. In a series of experiments the fishes were starved for about 1 $^1/_2$ month at a temperature of 7°—8° C. Thereafter the temperature was slowly raised to about 18° C, while the animals were given food at the same time. Other fishes were kept at 0°—7° C from Nov. 30 1955 to April 3, 1956, but were fed during the whole time. The scales of these fishes were treated according to STOELTZNER's method. In doing so the times of reaction were kept constant: cobaltous nitrate 2 min., washing 1 min., and ammonium sulphide $^1/_2$ min. It was intended afterwards to acclimatize the fishes to a higher temperature, but they died.

Finally the growth has been followed of a number of fishes from March to September at a temperature of 18°—20° C. Simultaneous controls of the scales were carried out. In addition scales from newly caught fishes have been treated according to STOELTZNER's method with larger intervals during the course of the whole year.

Results. Preliminary observations on the scales of roach treated according to STOELTZNER had indicated that within the cranial portions of the scales the width of the zone of growth deccreases or even drops to nothing, especially in winter. It was observed also that the osseoid was broad during summer. The former observation is corroborated by the experiments with fishes which were kept in cold water during winter, even if the width of the osseoid was small, and varied between different scales. At the termination of the experiments the zone of growth was altogether missing in some cases, or considerably narrower than in fishes which were growing.

Fishes which had starved in cold water could be kept alive for about 2—3 weeks after their transfer into warm water. After about 10 days a feeble, but distinct increase in the width of the zone of growth could be noticed.

Scales of fishes which are actually growing *always* exhibit a wide zone of growth. Of particular interest is the case of two fishes in an aquarium (18°—20° C) of which one became 0.5 cm longer, while the other did not grow at all. A control examination proved the latter to contain a *Ligula.* The scales of the first fish showed a wide zone of growth, whereas those of the latter resembled most closely scales of fishes caught during winter.

The above reported experimental results are not entirely corroborated by the results from staining of scales of freshly caught fishes. Thus, e.g., scales with a narrow zone of growth have been encountered during summer. This can be due to different causes: the fish in question may not be healthy, it may be attacked by parasites or the like, or the scale may be derived from a comparatively large fish. It is worth mention that the observation that larger roaches grow much more slowly than the smaller is of a late date.

Discussion. The material at hand shows that fishes in the state of growth possess scales with a wide zone of growth. The increase in width can be derived from either of the two components, the osseoid zone or the zone of calcification. In the majority of cases both increase in width simultaneously, but occasionaly the zone of calcification is narrow in spite of a relative great width of the osseoid zone.

The increase in width of the osseoid zone during the summer evidently causes a certain retardation of the calcification in relation to the synthesis of the proteins. In this case striae are formed which usually run into the osseoid zone, and end there. The calcification of the existing matrix on the other hand continues even after the termination during autumn of the production of proteins. In this latter case earlier preformed striae are calcified, but the striae come to terminate freely in the interior of the osseous layer, since no simultaneous apposition of proteins takes place. At the same time the wave of calcification continues towards the edge of the scale.

On the basis of earlier observations on the formation of striae under regeneration after the resorbtion of scales, when striae were formed shortly after the begin of the synthesis of proteins, the origin of the "winter ring" can now be described in the following way: In the autumn, when the growth of the fish and of the scales has ceased, the calcification of the osseoid zone with the striae occurring in it continues. When the calcification passes these striae, they are left behind as low striae which terminate freely upon the surface of the osseous layer. This is due to the circumstance that the stria does not run exactly parallel with the outer edge of the osseoid zone, and therefore is not developed simultaneously throughout its entire length, but from a single point by a gradual growth around the scale. The first stria is preformed, when growth is resumed. This stria is complete, since its curvature is determined by the outline of the calcified scale. The influence of the interrupted striae upon the process is small, as pointed out above. A few more striae are formed close to each other, but with the increase in width of the osseoid zone also the striae are formed at gradually increasing intervals. This introduces the formation of the "summer ring".

On this account the application of STOELTZNER's method to the scales of a certain individual should be able to tell, whether or not the fish is in the state of growth at that time. The method is easy and fast in application, the whole process being carried out in a test-tube in a few minutes. The boundary between the zone of calcification and the osseous layer is very distinct, but on account of the small differences the choice for analysis of the most suitable scales is advisable. It is thus necessary to know which scales are most suitable in each species, and what parts of the scale give the best results. In this investigation on the roach mainly scales from the area above the lateral line in the anterior half of the fish have been used. Of these scales the sides of the unexposed part have proved the most suitable. Finally it is necessary by an examination of a greater number of scales from fishes at different seasons entirely empirically to determine the ratio between the width of the zone of growth and the rate of growth.

Summary

The extremely numerous investigations into the development of the scales of fishes which have been published have not resulted in a greater measure in widened information on the subject. On the contrary, the resultats of examinations, also those carried out at the same time, have not agreed even in the main points. This can partly depend on technical difficulties, inherent with the object, partly on deficient general information about the way in which the extracellular components of the connective tissue are formed, and partly on the great differences existing between the different species examined. This last point implies that it is not admissible to assume the applicability of results obtained from one type of scales to every other type.

The problem of the origin of the striae which is of the greatest importance for practical studies has given rise to widely divergent hypotheses. These have in all cases been based upon general, non-specific histological stainings, while practically no attempts have been made to approach the problem by an experimental analysis.

In this investigation specific histochemical methods have been applied to the study of the scales of fishes for the first time. By this procedure it has been possible to elucidate the presence of acid mucopolysaccharides in the osseous layer and their connection with the calcification. The zone of growth of the scale and the scale-building cells have been identified. In this way it has been possible to follow the development of a stria from the germ stage to the stage of full development. The discovery of the great importance of the calcification for the morphological configuration of the stria was surprising. On the basis of these facts together with the experimental results both the mechanism of the formation of the striae and the development of the "winter ring" have been drawn up. The striae are supposed to be the results of a compression of the scale-forming assemblage of cells between the dermis in the scale pocket and the calcified scale. The compression is due to the increase in volume of the cells on their transformation into the active stage. The accumulated pressure induces the formation of a fold in which the stria is formed. The closely set striae of the "winter ring" are supposed to be formed at the resumption of growth in spring and as a result of the small width of the osseoid zone, since the distance between the striae is, within certain limits, proportionate to this width. Thus a determination of the width of the zone of growth makes it possible roughly to decide whether or not an individual is in a state of growth.

Several earlier authors are of the opinion that the fibrillary plate and the osseous zone have different origins. In the present investigation it has,

however, been possible to demonstrate that osseous layer as well as fibrillary plate are extracellular formations which in addition merge into one and into the same germ structure at the periphery of the scale. The absence of metachromatic substances renders the fibrillary plate unique among calcified tissues. By the absence of alkaline phosphatase and glycogen in the scale-forming cells also the scale as a whole exhibits a simplified type of the formation of bone.

The main interest has been directed towards the formation of the striae and the development of the scale. In this connection the experimental study of the formation of the striae has yielded certain results of a more general physiological bearing. Strong arguments have been advanced for the opinion that the fishes are unable to synthesize their entire requirement of vitamin C. Also vitamin D is necessary in order to prevent damages in the exoskeleton of the fish. An examination of the serum calcium indicates a strict governing of the metabolism of calcium in the fish.

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Literature

AGASSIZ, L. *Ann. Sci. Nat., Ser. 2, 14, 97,* 1840.
BAUDELOT, E. *Arch. Zool. Exp. Gen., 2, 87 o. 427,* 1873.
BECHER, H., K. HOEGEN, and G. PFEFFERKORN. *Acta Anat. 20, 105,* 1954.
BECKMAN, W. C. *Pap. Mich. Ac. Sci. Arts Lett. 28, 281,* 1942.
BEVELANDER, G. and P. L. JOHNSON. *J. Cell. Comp. Physiol. 25/26, 25,* 1945.
— — *Anat. Rec. 108, 1,* 1950.
— — *J. Dent. Res. 24, 123,* 1955.
BIERING, A. *Acta Ped. 31, 235,* 1943.
BODANSKY, A., R. M. BAKWIN, and H. BAKWIN. *J. Biol. Chem. 94, 551,* 1931.
BOURNE, G. H. *Quart. J. Exptl. Physiol. 32, 1,* 1943 (a).
— *J. Physiol. 102, 319,* 1943 (b).
— *The Biochem. and Physiol. of Bone, New York,* 1956.
BRADFIELD, J. R. G. *Exptl. Cell Res. Suppl. 1, 338,* 1949.
— *Biol. Revs. 25, 113,* 1950.
CAGLIOTI, V., A. ASCENZI, and M. SCROCCO. *Experientia 10, 371,* 1954.
CASPERSSON, T. *Symp. Soc. Exptl. Biol. 1, 127,* 1947.
CRICHTON, M. I. *Fish Board Scotl. Salmon Fish. 4, 1,* 1935.
DAHL, L. *Proc. Soc. Exptl. Biol. Med. 80, 474,* 1950.
DANIELLI, J. F., H. B. FELL, and E. KODICEK. *J. Exptl. Pathol. 24, 196,* 1943.
DELSOL, M. *Compt. Rend. Soc. Biol. Paris, 147, 1184,* 1953.
DIETRICH, M. A. *Quart. J. Micr. Sci. 94/1,* 1953.
DOMBROWSKI, H. *Biol. Zentr. Bl. 72, 182,* 1953.
DZIEWIATKOWSKY, D. D. *J. Biol. Chem. 178, 931,* 1949.
— *J. Biol. Chem. 189, 187,* 1951 (a).
— *J. Exptl. Med. 93, 451,* 1951 (b).

FABER, M. *Arch. Pathol. 48, 342,* 1949.

FACH, M. *Zschr. Anat. Entw. Gesch. 105, 288,* 1936.

FELL, H. B. and J. F. DANIELLI. *Brit. J. Exptl. Pathol. 24, 196,* 1943.

FERNANDEZ-MORAN, H. and A. ENGSTRÖM. *Nature 178, 494,* 1956.

FOLLIS, R. H. *Bull. Johns Hopkins Hosp. 89, 9,* 1951.

FONTAINE, R. and PORTIER. *Compt. Rend. Ac. Sci. 193, 1218,* 1931.

FRAISSE, B. Die Regeneration von Geweben und Organen bei Wirbeltieren, besonders Amphibien und Reptilien. Kassel-Berlin, 1885.

GIANGROSSO, G. *Boll. soc. ital. biol. sper. 14, 522,* 1939.

— — *14, 525,* 1939.

— and C. GANGANTINO. *Boll. soc. ital. biol. sper. 14, 531,* 1939.

GLICK, D. Techniques of Histo- and Cytochemistry, New York, 1951.

GOMORI, G. *Am. J. Pathol. 19, 197,* 1943.

GREEN, E. H. and R. W. TOWER. *Bull. U. S. Fish Commis. 21, 97,* 1901.

GÖSSNER, W. *Zschr. wiss. Mikroskopie u. mikr. Tech. 61, 377,* 1954.

HAEMPEL, O. *Zschr. Fischerei 25, 477,* 1927.

HANCKE, H. *Zschr. Chir. 245, 530,* 1935.

— *Klin. Wochschr. 15, 1121,* 1936.

HARRIS, J. H. and S. N. RAY. *Biochem. J. 26: 2, 131,* 1932.

HASE, A. *Jen. Zschr. Naturwiss. 42, 607,* 1907.

— *Anat. Anz. 40,* 1911.

HASS, G. M. *Arch. Pathol. 35, 275,* 1943.

HELLER, M., F. C. MCLEAN, and W. BLOOM. *Am. J. Anat. 87, 315,* 1950.

HELLER-STEINBERG, M. *Am. J. Anat. 89, 347,* 1951.

HOFFBAUER, C. *Allg. Fisch-Ztg. 19,* 1899.

— — *25,* 1900.

HOROWITZ, N. H. *J. Dental. Res. 21, 519,* 1942.

JACKSON, S. F. *Nature 173, 950,* 1954.

JONES, J. W. *Fish. Invest. Ser. I/5, nr 7,* 1953.

KLAATSCH, H. *Morph. Jahrb. (Gegenbaur) 16, 97,* 1890.

KROON, D. B. *Acta Anat. 15, 317,* 1952.

LAUBER, H. J. *Beitr. klin. Med. 161, 565,* 1936.

— H. NAFZIGER, and T. BERSIN. *Klin. Wochschr. 16, 1313,* 1937.

LILLIE, R. D. *Bull. Int. Ass. Med. Mus. 32, 83,* 1951.

LINDAHL, P. E. and O. WALLIN. *Arkiv för Zool. 8/8, 561,* 1955.

LOGAN, M. A. *J. Biol. Chem. 110, 375,* 1935.

LORCH, I. J. *Quart. J. Micr. Sci. 88, 367,* 1947.

— — *90, 183,* 1949 (a).

— — *90, 381,* 1949 (b).

MANDL, L. *Am. Sci. Nat. Ser. 2, 13, 62,* 1840.

MASTERMAN, A. T. *Fish. Invest. Ser. I/1, nr 3, 4,* 1923.

MCCHESNEY and GIACOMINO. *J. Clin. Invest. 24, 680,* 1945.

MCDONALD, M. *J. Gen. Physiol. 32, 39,* 1948.

MCGEE-RUSSELL, S. M. *Nature 175, 301,* 1955.

MOOG, F. *Biol. Bull. 86, 51,* 1944.

— and E. L. WENGER. *Am. J. Anat. 90, 339,* 1952.

MORGAN, T. H. *Arch. Entw. Mech. 10,* 1900.

MÜLLER, K. *Inst. Freshwater Res. Rep. 34, 78,* 1953.

NARDI, F. *Arch. Entw. Mech. 133, 621,* 1935.

NEAVE, F. *Trans. R. S. Canada 30,* 1936.

— *Quart. J. Micr. Sci. 81, 541,* 1940.

Neuman, W. F. *Trans. Jos. Macy Conf. on Metabolic Interrel. 2, 32,* 1950.
— and M. W. Neuman. *Chem. Revs. 53, 1,* 1953.
Nusbaum, J. *Anat. Anz. 30, 297,* 1907.
Paget, G. W. *Fish. Invest. Ser. II, Sea fish. Vol. IV, nr 3,* 1920.
Pevsner, V. *Zool. Anz. 68, 303,* 1926.
Pflugfelder, G. *Arch. Entw. Mech. 146, 115,* 1953.
Pickford, G. *Bull. Bingham Ocean. Coll. 14/2, 5,* 1953.
Pincus, P. J. *Calif. State Dent. Ass. 26, 16,* 1950.
Porter, K. R. *Trans. Jos. Macy Conf. Connect. Tiss. 2, 126,* 1951.
Pritchard, J. J. *J. Anat. 84, 236,* 1950.
— — *86, 259,* 1952.
— in: Bourne. *Biochem. and Physiol. of Bone, 196,* 1956.
Rasquin, P. and L. Rosenbloom. *Bull. Amer. Mus. nat. Hist.* 1953.
Reddi, K. K. and A. Norström. *Nature 173, 1232,* 1954.
Robinson, R. *Biochem. J. 17, 286,* 1923.
Roche, M. J. and E. Bullinger. *Bull. Soc. Chim. Biol. 21, 166,* 1939.
— J. Collet, and M. Morgue. *Enzymologia 8, 257,* 1940.
— and M. Morgue. *Compt. Rend. Acad. Sci. Paris, 214, 809,* 1942.
Rubin, P. S. and J. E. Howard. *Trans. Jos. Macy Conf. on Metabolic Interrel. 2, 155,* 1950.
Ruth, E. B. J. *Stain. Technol. 21, 1,* 1946.
— *Am. J. Anat. 80, 35,* 1947.
Ruyter, J. H. C. *Acta Anat. 16, 209,* 1952.
Salbey, R. *Arch. Anat. Physiol. Wiss. Med. 729,* 1868.
Sauer, V. *Arch. Entw. Mech. 132, 1,* 1934.
Savage, E. E. *Fish. Invest. Ser. II, Sea fish. Vol. 4, nr 1,* 1919.
Schereschewsky, H. *C. R. Ac. Sc. URSS 29/2, 165,* 1940.
Schmidt, W. J. Die Bausteine des Tierkörpers in polarisiertem Lichte, 310, 1924.
— *Zschr. Naturforsch. 2 b, 233,* 1947.
— *Zschr. Mikr. 60, 1, 1951.*
Schäperclaus, W. Fischkrankheiten, 2nd ed. Braunschweig, 1941.
Segerstråle, C. *Acta Zool. Fenn. 15, 9,* 1932.
Setna, S. B. *J. Univ. Bombay (Biol. Sci) 2: 5, 17,* 1934.
Signer, R., F. v. Beust, and U. A. Corti. *Schw. Zschr. Hydrol. 13, 31,* 1951.
Skjerven, O. *Acta Endocrin. 14, 52,* 1953.
Sobel, A. E., J. Cohen, and H. Kramer. *Biochem. J. 29: 2, 2640,* 1935.
— *Trans. Jos. Macy Conf. on Metabolic. Interrel. 4, 113,* 1952.
Steenbock, H. and Black. *J. Biol. Chem. 64, 263,* 1925.
Stoeltzner, W. *Wirch. Arch. Pathol. Anat. 10/180, 362,* 1905.
Sylvén, B. *J. Bone and Joint. Surg. 29, 973,* 1947.
Taylor, H. F. *Bull. Bur. Fish. 34, 289,* 1914.
Tesch, W. *Zschr. Fischerei, 4, 322,* 1955.
Wallin, O. *Quart. J. Micr. Sci. 97, 329,* 1956.
Wassermann, F. *Am. J. Anat. 94, 399,* 1954.
Williamson, W. C. *Philos. Tr. Royal Soc. London 139, 435,* 1849.
Wunder, W. and H. Schimke. *Arch. Entw. Mech. 133, 245,* 1935.
Wunder, W. *Arch. Entw. Mech. 143, 396,* 1949.
Yamada, J. and S. Saburo. *Mem. Fac. Agr. Hokkaido Univ. 2, 354,* 1953.

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