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MONOGRAPH OF THE COREGONINES OF SWITZERLAND.

A CONTRIBUTION TO THE PROBLEM OF THE FORMATION OF NEW SPECIES.

By P. Steinmann

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PAUL STEINMANN:

A MONOGRAPH OF THE COREGONINES OF SWITZERLAND

A Contribution to the Problem on the Formation of New Species.

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MONOGRAPH
OF THE SWISS COREGONINES

A Contribution to the Problem on the Formation of New Species

by Paul Steinmann, Aarau

Received on June 15, 1950

INTRODUCTION

On instructions from the Cantonal Directorate of Forestry of the Canton of Berne I undertook an investigation of the Coregonines of Lake Thun from 1935 to 1938. Subsequently it became necessary to extend these investigations to other lakes in Switzerland. Various Cantons showed themselves desirous of obtaining analyses and advice concerning the management of their lakes. The question of the artificial breeding of Coregonines caused considerable discussion and for many years occupied the attention of the Scientific Commission of the Swiss Fishing Association. In some places serious doubts were voiced in the matter of the random transfer of coregonine material from lake to lake. There were questions concerning the rate of growth of individual types, conservation seasons, as well as other conservation methods, sizes and types of nets and other similar problems. Finally I arrived at the decision to make the whole complicated coregonine problem the subject of an all-encompassing study. In this connection I was particularly interested in

the systematical-genetical problem, the ecological behaviour of the Coregonine race and finally the economic question dealing with suitable measures for the improvement and increase in the number of coregonines. Having concluded this study I am fully conscious of the fact that much remains unexplained. Nevertheless I hope that some aspects have become somewhat clearer and that there will be some practical benefits from our work. We should not forget that the coregonine are to-day, as before, the economically most important fishes of the larger lakes of our country. Thus their conservation and care must be considered an urgent task of the present.

Our investigation called for a considerable organization which could be achieved only with the selfless help and co-operation of various colleagues and fellow-specialists. Financial support was given by the Federal Inspectorate for Forestry, Hunting and Fishing and by the Swiss Fishing Association. I am also obliged to my colleagues from the Scientific Fisheries Committee for their valuable help as well as to the Fisheries Wardens who work at most of our lakes, as well as to the Scientific Instutes at Langenargen and at Stead near Constance, to many Cantonal officials, experienced professional fishermen, fish breeders and fishing associations. All in all thousands of fish passed through the hands of the investigators during these 15 years. Hundreds of them

were photographed, measured and statistically tabulated. The following gentlemen were particularly helpful in the subsequent investigations of the material: Dr. Muckle, Staad; Dr. Numann, Dr. Grim and Dr. Kriegsmann, Langenargen; Dr. Florin, St. Gallen, Dr. Gubler, Zürich; and Dr. Kupka, Graz. I am particularly obliged for the generous help given to me by Mr. A. Mathey-Doret, Federal Inspector of Fisheries, Berne and Mr. F. Grivaz, Forestry Inspector at Lausanne, as well as Prof. Dr. M. Auerbach at Staad. Among others the following devoted their efforts to the calculation and measurement of the research material: Mrs. Müller-Arber, H. Britschgi, J. Fluck, H. Stauffer and H. Ambuhl. I find it impossible to mention by name all the gentlemen who have helped and advised me in the compilation of this work.

METHODICAL

Generally the usual biometric methods based on indices have proved themselves to be satisfactory for the differentiation of types. It is thanks to these methods that the fluctuating variability of the coregonines is so clearly expressed in our tables. It is, however, impossible to achieve satisfactory collection results without obtaining the relatively scarce juvenile forms as well as specimens of advanced age. I was, therefore, required to undertake special measures of catching

material of
in order to obtain/the greatest possible variety. In all cases I attempted to get examples of extremely large and extremely small specimens and by this method I arrived at a much greater breadth of variation of indices than that recorded by my colleagues in previous years. I also made a fundamental point of not avoiding the uncertain intermediate forms from my statistics, a practice which had often been followed in the past. Above all I attempted to supplement the morphological investigations by means of ecological ones. I also made use of every opportunity that offered itself to take up complimentary serological and zytological studies in conjunction with any of my fellow specialists who were interested in these fields. Finally I was in a position to carry out certain breeding experiments over a period of several years in order to determine the modificability of the coregonine tribes on one hand and the possibilities of their hybridization on the other hand. In the serological investigations I was fortunate to have the help of

a
Dr. Gubler, Zurich. After/discussion concerning the goals of our study we only had to deliver the necessary materials to him. The chromozomal studies were conducted by Dr. Kupka, first in Zurich and later on in Graz. Together with him we tested the study material at various bodies of water and he then conducted the histological analyses at the Zoological Institutes of Zurich University and

the University of Graz. We deal with the results of this research in the genetico-systematic part of our study and at this time we would only like to state that the hybridization was so completely successful and that there was no hybrid sterility (bastard sterility) of any degree and that by means of serological tests it was possible to prove the very close relationship even of the most extreme ecotypes and that the subsequently investigated populations of Lake Zürich, Lake Lucerne, Lake Constance—and later on also of Atter Lake, showed considerable irregularities in the chromosone distribution so that Kupka is of the opinion that this liability of genes corresponds to the variability of types. From the zytological point of view there is reason to consider the Coregonus as a "superspecies" (~~of~~ a polytypical species)which is in the process of differentiation.. I myself have on the basis of my morphological and ecological field studies arrived at the very same conclusion. From year to year I became increasingly convinced that the "species formation" within the genus Coregonus was in full swing and that for animo-geographical and ecological reasons, this was a unique possibility to ~~study~~ obtain an insight into the form-creative workshop of nature.

Illustration fig.1. The coregonine waters of the northern edge of the Alps which are the subject of our study.

1. Lac du Bourget
2. Lac d'Annecy
3. Lake Geneva, Lac Leman
4. Lac de Joux

5. Lake Neufchâtel
6. Lake Bienne.
7. Lake Murten
8. Lake Brienz
9. Lake Thun
10. Sempach Lake
11. Baldegg Lake
12. Hallwil Lake
13. Lunner Lake
14. Sarner Lake
15. Lowerzer Lake
16. Lake Lucerne
17. Ageri Lake
18. Zuger Lake
19. Lake of Walen
20. Lake Zurich
21. Pfaffiker Lake
22. Greifen Lake
23. Lake Constance
24. Lower Lake

Generally speaking, the commonly used biometric methods based on indices have stood the test of time. Thanks to these methods the fluctuating multiplicity of the coregonine fishes is clearly expressed in our tables. It is, however impossible to do without the not so easily obtainable collection of immature and very old specimens, and this obliged me to adopt special measures in order to catch and collect material of the widest possible variety. I also invariably attempted to obtain extremely large and extremely small specimens and thus I frequently arrived at a considerably wider spread of variations of indices than my colleagues did in the course of the preceeding years. As a matter of principle I also attempted to avoid excluding uncertain intermediate forms from the statistical compilation, although this practice has frequently been followed in the past. Above all, I attempted to supplement the morphological investigations by means of ecological ones. I also made use of every opportunity to complement the work by means of serological and cytological studies. In this I was aided by colleagues who specialized in these fields and who were interested in this work. Finally I was able to conduct several breeding experiments covering a period of years in order to test the modifiability of coregonine breeds and the possibilities of hybridization. In the matter of the serological analyses I was fortunate to be able to count upon the help of Dr. GUBLER (ZURICH). After some preliminary conferences dealing with the aims of our work we were only required to forward our material to him.

The chromosone studies were conducted by Dr. KUPKA, first at ZURICH and later on at GRAZ. We were able to check the material to be studied in various bodies of water with him and he then undertook to conduct the histological investigations at the Zoological Institutes of the Universities of ZURICH and GRAZ. We will deal with the results of this research in greater detail in the genetico-systematical part of our study and at this point we would merely like to state that the hybridization was successful in every single instance, without any degree of hybrid-sterility ever becoming apparent; that it was possible serologically to prove the extraordinary close relationship of even the most extreme eco-types; that in the course of the subsequently investigated fish populations of the Lake of Zürich, Lake Lucerne and Lake Constance- and later also Atter Lake in Austria- considerable differences in the chromosone distribution could be ascertained, so that KUPKA is of the opinion that this lability of genoms corresponds to the (great) variety of types. From the cytological point of view it would appear reasonable to consider the forms covered by the term "coregonus" as a "collective species" (polytypical species) in the process of differentiation. Year after year my morphological and ecological practical field studies tended to support the validity of this concept. I gained the conviction that the "formation of species" of the genus Corregenus is in full swing and that a study of this process offers a zoographically and ecologically unique opportunity to gain an insight into the workshop of nature in the course of its creation of new forms.

A CONTRIBUTION TO THE HISTORY OF THE SYSTEM.

The earliest fish experts already included the coregonine fishes (called "Felchen" in German, "Velchones" in Monastery Latin) among the"salmonides", i.e. among the salmon and trout-like species. The genus was even originally included in the category of "Salmo" but then separated from it as "Corregonus" by ARTEDI in 1738 and in this sense it was included by LINNE into his system of 1758, at first however only as a sub-group (Coregoni Thymallus /greyling)

We were also in the possession of several valuable reports concerning coregonine fishes antedating this clarification of the system; some from French sources: BELONIUS (1553) RONDELET (1553) and then from Swiss and German sources; MANGOLIT (1557) and Conrad GESSNER (1558)

BELONIUS knows but one coregonine fish, the "Lavaretus" which he describes as it is found in Lake Geneva. Lac du Bourget and Lac d'Aiguebelette. The name Corregonus lavaretus was also adopted by LINNE (1758) and later by CUVIER and VALENCIENNES (1848) and incorporated in their system. If it should be proved that the Central European coregonine fishes actually represent a single species, then according the the rules of nomenclature, this name would have to apply to all of them. The first differenciation was the work of RONDELET, who separated the "Lavaret" of Lac du Bourget from the "Fera" of Lake Geneva.

MANGOLT and GESSNER, who based the selves on the core-

gonine fishes of Lake Constance, also differenciated among the various coregonine fishes, evidently according to the custom then prevailing among the fishermen of Lake Constance and GESSNER thus arrived at no less than six types (species?) of coregonines.

Today the identification and systematic arrangement of GESSNER's coregonine species would present great difficulties, for the descriptions recorded by this scientist appear to be based, at least in part, not on his own observations, but rather on other sources, and his illustrations do not suffice to enable us to arrive at definite conclusions.

MANGOLT's "Edles Fischbüchlein" (Noble Little Book of Fishes") (the edition I used is anonymous) very fittingly comments on these "species": "There is however a considerable difference among the "Felchen" depending on their habitat- while some dwell in sandy (waters)- and these are called "Sand" or "Adelfchen" (sand or noble coregonines) others however inhabit the bottom and the depths, and they are called "Blaufelchen" (Blue coregonines"/ just as these "Felchen" differ in their names/ so they also differ in their nature. For when a "Sandfelchen" is hit / it floats upwards/ but when the "Blaufelchen" is hit / it sinks to the bottom. "

MONGOLT is obviously thinking of peculiarities caused by the environment and if he were alive today he would probably refer to them as "local variations" or modifications. How little credence he gave to the effective value of the vernacular names is evident from the fact that he considered some designations as being valid for one and the same fish:

"Seel" "Stub" and "Gandfisch" is only one fish/ but it changes its name.

On the Lake of Zurich they are called "Albelen" (Aburin), coming either from "albetudine" i. e. the white of the scales and the meat: or from the word "halb" (half) /that is to say "Halbeln" (little halves)/ because they are half matured fish. In the third year they are called "Gangfische" ("Going" or "wandering" fish-)....etc."

MANGOLT further differenciates:

"Sandgangfische" (sand wandering fish) which in maturity are called "Sand" or "Adelfchen" (sand or noble coregonines).

"Grüne Gangfische" (green wandering fisch) which mature into "Blaufelchen" (blue coregonines) and ""eisse Gangfische" (white wandering fish) which remain "Gangfische" (wandering fish).

In addition to these MANGOLT also describes the "Kirchlein" (little church?):

".... this being a white scalefish and shaped like the "Gangfisch" (wandering fish)/ they have a large belly/ and grow to half the size of "Gangfisch". They dwell in the depths and spawn in the Summer/ and should be cooked the same as coregonines."

Without specifically mentioning it in detail, GESSNER appears to base himself on the data compiled by MANGOLT, with whose books he was familiar. But he attempts to proceed from there, by identifying and comparing and equating the specimen found in Lake Constance to certain types found in other lakes.

1. The first such series according to GESSNER consists of the "Adelfisch" (nobility fish), which he also calls "edle Albelen (burin)" (i.e. noble"äburin")/see above- or "weisser Blauling" (white "blue shad"?) or "blue char".

It is identified with BELONIUS' "Lavaretus".

2. In second place GESSNER ranks the "Blawling" (perhaps a corrupted version of an adjectival noun formed from 'blue'-trans.) the "Albula coerulea", a term which he evidently applies to the type generally known today as "blue coregonines of Lake Constance". Among his German trivial names some doubtful cases of nomenclature can be encountered: "Bratfisch" /"frying fish"/ (evidently originating from the Lake of Zurich: MANGOLT described the "blaufelchen (blue coregonine) as a particularly good fish for frying. In addition to this GESSNER also calls this fish "Felcken" or "Felchen" (coregonine). "Balhenen" (evidently "Balchen") "Baal" (reminiscent of "Palee"), "Albock" "Renchen" and "Gangfisch" (wandering fisch). GESSNER's writings do not clearly indicate on which lakes the different vernacular names were current. GESSNER appears to have been most familiar with conditions on the Lake of Zurich and on Lake Lucerne. GESSNER equates the "Grossfelchen" (large or great coregonine) of Lake Lucerne in his day, which would correspond to the present-day "Edelfisch" (noble fish), to the "Blawling". He appears to consider the small coregonines to be young "Edelfische" (noble fishes). He calls them "Nachtfisch" (night fisch) and later "Edelspitzling" (pointed noble fish),then

then "Edelfisch" (noble fish) and finally "Balhen", he thus clearly indicates that he believes that the "Adelfisch" (nobility fish) or "Sandfelchen" (sand-coregonines) of Lake Constance are not to be found in Lake Lucerne.

3. Albula lacustris, sp. alia, also called Farra or Ferra;-it is impossible to identify it positively , but the term evidently includes the form called "Fera" by BELONIUS. and ROND'LET. GESSNER also reports finding this from in Lake Geneva and adds that it is very similar to the "Adelfisch" of Lake Constance. Its length is given as one ell (approx. 2 ft.)

4, Albula parva, also called "Albulen" or "Weissgangfisch" (white wandering fish). Most probably this means the "Gangfisch" (wandering fish) of the Untersee (lower section of Lake Constance) although GESSNER only reports of one incidence on the u per part of the Lake of Zurich. It appears that this is the "Albeli" which to this very day passes back and forth through the narrows at RAPPERSWILD in order to get from the upper to the lower la-ke.

5. "Hägele" or "Hägling" (Albuma minima), which to GESSNER evidently was the dwarf-coregonine of the Lake of Zurich, a species which in the meantime has become very rare. This type of fish appears to have been very abundant and was caught in great quantities (large catches).

6. Angelin, a tiny white dwarf-coregonine, which GESSNER only mentions to have found on the Lake of Bienne.

GESSNER's fund of knowledge concerning the distribution of coregonines in Switzerland would appear to be quite spotty to judge by the above information, and his experiments to establish interrelationship between the forms found in different lakes must be evaluated with great precaution. He also

a pears to have received no more precise details from his contemporaries RONDELET and BELONIUS. His reports concerning the "Fera" appear to be based on hearsay and he does not seem to h ve had any comparison material in his possession.

The famous naturalist Conrad GESSNER was considered an outstanding authority for many decades and as a result the scientific systems of the 18th century were strongly influenced by him. Nevertheless, the nomenclature used to designate GESSNER's forms, which appear in journals indicate the existence of considerable c nfusion in this matter. At the beginning of the 18th century Johann DE MURALT, fro ZURICH wrote a study dealing with birds, fishes and snakes. (De avibus, serpentibus Figuri-170 /10-) This researcher appears to lea heavily on GESSNER's works. He reports that the "Hagling" is quite ravenous and claims that this is the reason why it can be easily caught with a fishhook. DE MURALT's "Blauling" appears to include the "Sand" and "blue" coregonines mentioned by other authors, just as it has at a later date never been possible to distinguish "floating" from "Botom" types among the coregonines of the Lake of Zurich. The "albila coruela sive mugil lacustris" or "flaco" are praised for the excellent quality of their meat. The impossibility of drawing sharp lines of division is significantly emphasized by MURALT's words:

"Inter hos tamen pisces magnum quoque est discrimen pro diversitate et loci et alimenti..., in omnibus fere Helvetiae lacubus rereriuntur, sed diversa habent nomina".

Other 17th century books dealing with fishes also contain references which cast doubt upon the justification and validity of the then current specie names. Thus it has been repeatedly maintained, but also vehemently denied that the "Bondelles" of Lake Neuchatel are in fact young Palees (IACARDE and others)

We have not encountered any systematic work of revision dealing with the systematics of coregonine classification which were compiled during the era of the grea systematician LINNE or his followers.

In addition to the "Coregonus (Salmo) lavaretus, LINNE (1766) appears to knwo only the species albula "kleine" (small) "Maräne" (Coregonus mara ne/?/ or lake Coregonus sardinella/?/ among central European coregonines. This last fish was subsequently described in greater detail by Bloch who gave this species the name maraenula. In 1777 B. HARTMANN, a physician, fro. ST. GALLEN, compiled a reliable description of the "Bodenseeblaufelchen" ("Blue coregonine of Lake Constance", which BLOCH named Coregonus wartmanni in his honour. That makes two coregonines of German Switzerland which were more or less recognizably described by the turn of the century (1800): the "Blaufelchen" (Blue coregonine) and the ("sandfelchen) (sand coregonine) "Lavaret". Along with these two there appear for the time being, still somewhat nebulous, the "kleine" (small) Maräne and the "Kilch".

This system however was not found to be satisfactory and somewhat later the great French zoologist CUVIER addressed the following comment to the naturalists of Switzerland: "Nous devons desirer que les naturalistes suisses mettent de l'ordre dans ce genre, en donnant avec bonnes figures une liste exacte des noms que chaque poisson porte dans les different lieux"

*) Copy French quotation on page 116 of the German text".

For the time being this invitation of the French zoologist remained but a pious wish. The ichtyologists of the German speaking Cantons of Switzerland in particular have in the main limited their studies to readily available local fishes: Those from ZURICH dealing with the coregonines of the Lake of Zurich, while those from Lucerne, focused their attention on Lake Lucerne etc. This has resulted in valuable descriptions of local varieties, without however forming a scientific basis for an overall revision of the then invalid systems.

II. Period.

The coregon researches of the second half of the 19th century on the main continued to utilize the nomenclature used by the German specialist von SIEBOLD, and in the 20th century Victor FATIO of Geneva was the leading researcher, to whom all, or at least most of the others referred to. As a result there is no lack of misunderstood terms and errors, which on this occasion we can not follow up in detail. Many controversies concerning the validity or invalidity of names took place during this period. Some of them were very fruitful, others less so. But in these arguments the different authors always seemed to miss each others point.

In this connection we will limit ourselves to drawing the reader's attention to only four studies, the authors of which had considerable collections of comparison material at their disposal and who therefore attempted to establish a relationship between the coregonines of the different lakes.

These studies are:

1. 1827: HARTMANN G.L. "Helvetische Ichtyologie oder ausfuhrliche Naturgeschichte der in der Schweiz sich vorfindenden Fische" ("Helvetian Ichtyiology or Comprehensive Natural History of Fishes found in Switzerland")
(ZURICH-ORELL, FUSSLI & Co. /240 pages/).

2. 1858:HECKEL J., and KNER R. "Die Süsswasserfische der österreichischen Monarchie mit Rücksicht auf die angrenzenden Länder" ("Fresh-water fish of the Austrian Monarchy with Consideration of the Neighbouring Countries.")
(LEIPZIG- Wilh. ENGELMANN/388 pages/)

3. 1863: Von SIEBOLD C. T. E. "Die Süsswasserfische von Mitteleuropa" ("The fresh water fish of Central Europe")
(LEIPZIG).

4. 1890: FATIO V. "Faune des Vertebres de la Suisse". ("The Vertebrate Fauna of Switzerland)"Volume V "Poisons" ("Fishes")II (GENEVA and BASLE- H. GEORG.)

HARTMANN.

In accordance with the views prevalent at the time, HARTMANN differenciates between five "species" or "types" of coregonines, which he described in the following manner: No. 1 Grosse Maräne (coregonous maraena?)/ "Adelfisch" ("nobility fish") "Adelfelchen" ("nobility coregonine") "Sandfelchen" ("sand coregonine") "Weissfelchen" ("white coregonine") "Miesadler"(?) juvenile "Adelperle" ("nobility pearlfish") f. juve-

Hile "Seelen" ("souls"-?-)"Heuerling" ("this year's fish") "Maidel" ("maidens-?-") "Stüben" "Gangfisch" ("wandering fish"), "Sandgangfisch" ("wandering sand fish"-?-)"Renken", "Felchen"/.

According to HARTMANN this category also includes the "Bläuling" ("blue fish") or "Bratfish" ("frying fish") of the lake of Zurich and the Lake of Wallen, the "Ballen" or "Balchen" of the other Swiss lakes, in particular the "Krautbalchen" ("herb-balchen") from Lucerne the "Schwemmbalchen" ("pond-balchen"), "Steinbalchen" ("stone-balchen"), "Edelbalchen" ("noble balchen"), as well as the Palees of Lake Neuchâtel and the "Feras" of Lake Geneva. Latin: Salmo marana Bloch. Spawning period: November-December. Concerning the growth of this fish HARTMANN reports that it weighs approximately 500 grammes when 4 years old, 1500 grammes when 6 years old, and only very rarely more than 2000 grammes.

No. 2. "kilchen". "kilchen", "Kropffelchen" ("goitre" or "adam's apple coregonine"), "Kirchfisch" ("church fish") at that time only known to occur in Lake Constance. -Latin- Salmo maraena media Hartm..

Spawning period: September Growth: First capable of reproduction when three years old, weight at that time: 4 "half ounces" (i.e. approx. 70 grammes) length approx. 21 centimetres.

C. GESSNER suspected that the fish, which in Lake Constance was known by the name "Kilch", was the same as some of the coregonines found in the other Lakes, which at the time were called: "Butz" or "Husen" of the upper part of Lake of Zurich, "Alpken" of Lake Lucerne and "Angelin" of the Lake of Bienne.

No. 3. "Kleine Maräne" ("Wandering Fish") of Lake Constance, sometimes also called the "Weissgang Fisch" ("White Wandering Fish") and in some ancient documents, "Wattfisch". In other parts of German-speaking Switzerland, it is called the "Albula". It appears to belong to the same line as the "Gravenche" and the "Besole" of Lake Geneva -- Latin: Salmo maraenula Bloch.
Spawning period: December.
Growth: Mature for reproduction in the 4th year.
Weight 8½ ounces (approx. 144 g.)

No. 4. "Hagling". In Lake of Zurich "Hagling", Lake of Brienz "Brienzlig", near Lucerne called "Nachtfisch" ("Night Fish"). Latin: Salmo albula Hartm.
HARTMANN also reports finding it in Hallwil Lake; it is said NOT to occur in Lake Constance.
Spawning period: End of June and then again in November (?).
Growth: Maximum length 6½-7 inches.

No. 5. "Blaufelchen". ("Blue Corregonine"). Juvenile "Seelen" ("Soles"), in the first year "Heuerling" ("This year's Fish"), "Meidel" or "Midellfisch", in the second year "Stuben", in the third year as "Green "Gangfisch" ("Wandering Fish"), in the fourth year "Springer" ("Jumper") or "Halbfelch" ("Half Corregonine"), from the 7th year onwards as "Felchen" or "Blaufelchen" ("Blue Corregonine"). These fish were particularly valued in the monasteries and in monastery Latin they were called "velchones". The blue corregonine of the Lake of Thun was called "Albock", that of Lake Lucerne was called "Edelfisch" ("Noble Fish"). When young, it was called "Edelspitzlig" ("Noble Pointed One"). HARTMANN suspects that perhaps the "Palée" of Lake Neufchâtel and Lake Geneva also belong to this group. Latin: Salmo wartmanni Bloch.
Spawning period: 10-14 days during the second half of

November.

Growth: 2nd year: 4 inches 1 ounce (approx. 16.5 g.)

3rd year: 6 inches 2 ounces (approx. 33 g.)

4th year: 8-9 inches 8 ounces (approx. 132 g.)

(first recreation)

5th year: ?

6th year: ?

7th year: 14-15 inches 38-44 ounces (620-730 g.)

(The units of measurement and weight indicated appear to be local Swiss units -- Translator's Note).

HECKEL and KNER

HECKEL and KNER only differentiated between three types of corregonines:

1. "Blaufelchen" ("Blue Corregonine"): Coregonus wartmanni Cuv. Evidently neither HARTMANN nor HECKEL nor KNER were acquainted with the study on blue corregonines made by WARTMANNS in 1777. They and some of their followers based themselves on quotations from BLOCH, CUVIER-VALENCIENNES and others.

Synonyms: Salmo wartmanni Bloch, Salmo lavaretus Meiding, Palée noire Jurine, Coregonus palea Cuv. and Val., C. nilsoni Val., C. reisingeri Val., C. fera Jurine, They, at that time, were identified to be the "floating corregonines" of Lake of Zurich, Lake of Lucerne, Lake of Brienz, Lake of Thun, Lake of Hallwil, Lake of Sempach and Lake Neuchâtel.

HECKEL and KNER give very widely diverging data concerning the spawning periods. Size: 15-18 inches. Weight: 1½-2 pounds, occasionally 3 to 4 pounds.

One interesting detail is the statement that the fish live at great depths (up to 600 feet) in the lakes and that they only rise up to a depth of 60 feet during the spawning period. For this reason they are usually caught only during the spawning period!

2. "Sandfelchen" ("Sand Corregonine"): Coregonus fera Jur. Synonymous with the "Kropfling" ("Adam's Apple") of Atter Lake and the "Rindling" of Lake Traun and evidently also with the "Palée" of Lake Neufchâtel. It is strange that this fish is described as being of smaller size when compared to the blue corregonine, (14-15 inches, having a weight of ½ pound).

Spawning period: In December, at depths of about 40 feet.

3. "Kilchen": Coregonus acronius Rapp. Found in Lake Constance only.

Spawning period:

The authors were not well acquainted with the "Kilch". They only state that schools of it were encountered in the depths of Lake Constance, in particular in the region of Uberlingen and Langenargen. Its biology was quite nebulous.

VON SIEBOLD

The most significant achievement of the VON SIEBOLD epoch are the radical groupings which he introduced into the previously divergent systems of classifying corregonines. On the basis of long, extensive and strenuous investigations using what, for that time, was most extensive material, Von Siebold concentrated all Central European corregonines in three "species". In doing this he arrives at the same final result as HECKEL and KNER. Typical of this is his confession:

"In spite of all efforts that I have devoted to learning to differentiate between the three types of Alpine Coregonus, it is even today not easy for me to differentiate between the corregonine from the various Alpine lakes at the first glance because the profiles and

size relationships of the various parts of the bodies of this fish vary considerably, depending on their age and locale. But I find it even more difficult to decide whether the corregonine of the Alpine lakes of Central Europe should be united within one and the same species with certain coregonine forms of Scandinavia, or whether they should be entirely and specifically separated from them as an entirely specifically different species."

The following is a characterization of the coregonine types according to VON SIEBOLD:

1. "Blaufelchen" (Blue Coregonine) (Coregonus wartmanni Bloch = "Renke" or common Renke), the "floating renke" occurring in the main in free water regions and living on plankton exclusively.

2. "Sandfelchen or Bodenrenke" (Coregonus fera Jurine), found at moderate depths all the way to the shores along the lake bottoms.

3. "Kilch or Kropffelchen" (Coregonus acronius Rapp. = Coregonus hiemalis Jurine), the deep lake coregonines of Lake Constance and according to RAPP and VON SIEBOLD, also of Lake Geneva.

Evidently VON SIEBOLD failed to note that the Gravenche of Lake Geneva actually would have to be grouped among the floating coregonines and cannot be put in the same category with the "Adam's apple" corregonine of Lake Constance. It is, by the way, typical that VON SIEBOLD only recognizes a single floating coregonine as such. The so-called small floating coregonine form reported by later and earlier authors, he simply considers the "Gangfisch" ("Wandering Fish"), to be a juvenile blue coregonine. The "common Renke" is also said to occur in Lake Lucerne, Lake of Brienz, Lake of Thun, Lake Hallwil, Lake of Sempach and Lake Neufchâtel. All small types of coregonines reported from these lakes and given special

names are simply considered juvenile forms of the respective types of blue corregonines by VON SIEBOLD. He not only follows GESSNER, MANGOLT and others in calling the "Seelen" ("Soles") "Heuerlinge" ("This Year's Fish"), "Stuben" and "Gangfische", all young corregonines, but he specifically designates the six-inch long corregonine of Lake Zurich as "Hagling" and the half-grown ones as "Albeli", and the fully-grown ones as "Blauling". From his explanations it is quite apparent that he also wishes to have the small corregonines, such as the "Brienzlig", "Weissfischli", ("Small white fish"), and the "Nachtfisch" (Night fish) of Lake Lucerne, to be juvenile corregonines. The same applies to the "Lavaret" of Lake Geneva which -- just like the one of Lac de Bourget -- which he also likes to consider to be a blue corregonine. He completely refuses the attempt to identify the "Gangfisch" or similar small corregonines with the Nordic "Kleinen Marane" (small marane) or to connect the "Hagling" with the Coregonus albula found in Scandinavia. In this respect VON SIEBOLD differs from HARTMANN and SCHINZ.

FATIO

If researchers like VON SIEBOLD, LUNEL and others, in the course of the second half of the 19th century attempted a unification and simplification of the corregonine systematics then, on the other hand, the Geneva zoologist, FATIO, working in the last decade of the century, based himself on the numerous nomenclatures devised by the practices and developed a tendency of dividing the group into types, species and sub-species. The following is a compilation of his system:

Coregonus dispersus (the group of blue or floating corregonines);
Coregonus wartmanni Bloch
" annectus Fatio
" Exiguus Nusslin

Coregonus suidteri Fatio

Coregonus balleus (the sand corregonine or bottom corregonine group);

Coregonus asperi Fatio

" Schinzii Fatio

" acronius Rapp

" hiemalis Jurine

After extensive and long-lasting studies based on numerous specimens originating from the various lakes, Fatio classified the Swiss corregonine in the following manner to fit into his system:

Coregonus wartmanni Bloch:

the "Blaufelchen" (blue corregonine)of Lake Constance)

the "Blauling" (blue one) of Lake Zurich

the "Blauling" (blue one) of Lake Bienne

the "Albock" of Lake of Thun

the "Edelfisch" (noble fish) of Lake Lucerne

the "Edelfisch" (noble fish) of Lake Sarnen

the "Albock" of Lake Lungern

the "Albock" of Lake of Thun

the "Albock" of Lake of Brienz

the "Pfarrig" of the lower lake

the "Pfarrit" of Lake Bienne

(the "Balchpfarrit" of Lake Neufchâtel).

Coregonus annectus Fatio:

the "Ballen" of Hallwil Lake

the "Ballen" of Lake Baldegg

Coregonus exiguus Nusslin:

the "Gangfisch" of Lake Constance

the "Albeli" of the Lake of Zurich (including the "Hagling" = winter albeli)

the "Weissfisch" (whitefish) of Lake Lucerne

the "Kropfer" (Adam's Apple) and"Brienzlig" of Lakes Thun and Brienz

the "Kropfer", "Ferit" of the Lake of Murten
the "Bondelle" of Lake Neufchapel and Lake Biehne
the "Kropfer" and "Ferit" of Lake Neufchâpel and Lake Bienne
Coregonus suidteri Fatio:
the "Ballen" of Lake Sempach.
Coregonus asperi Fatio:
the "Albeli" of the Lake of Zurich, the "Buchbergalbeli"
the "Albeli" of Pfaffik Lake
the "Albeli" of Lake Greifen.
Coregonus schinzii Fatio:
the sand, or the white, corregonines of Lake Constance
the white corregonines or "Sandblaulig" (bluish sand fish)
of Lake Zurich
the "Balchen" of Lake Lucerne
the "Balchen" of Lakes Thun and Brienz
the "Palée" of Lake Murten
the "Palée" of Lake Neufchapel
the "Palée" of Lake Biel
the "Féra" of Lake Geneva.
Coregonus acronius Rapp:
the "Kilch" or "Kropfelchen" ("Adam's Apple" corregonine)
of Lake Constance.
Coregonus hiemalis Jurine:
the "Gravenche" of Lake Geneva

This system, which was closely linked to the local nomenclature was of little help to ichthyologists of the following decades. While it is true that Fatio's types are occasionally found in museums and can be re-examined and re-measured today, to approach the present-day corregonine material of the lakes of Switzerland on the basis of FATIO'S descriptions and to classify this material in accordance with the principles of the above systematics is an entirely hopeless task. My former assistant, Dr. W. OCCHMANN, has attempted to do so for

many months and finally he came to me, convinced that the variability of the coregonines is much greater than FATIO supposed and that we could not possibly speak of a discontinuous variability, much less of a possibility of drawing sharp boundaries.

It is true that in the following period the Swiss zoologists (ASPER, ZSCHOKKE, HEUSCHER, NUFER, BIRRER, SCHWEIZER, SURBECK, and others) attempted to use FATIO'S systematics, but there always appeared difficulties in determination. Types were found which could not be exactly classified no matter how hard one tried, and usually one sought help by calling them "bastards" (hybrids), or simply considering them the result of the numerous exchanges of fish stock which had taken place between the various Swiss lakes in the course of efforts of "improving the breed" or "refreshing the blood stock".

III PERIOD

The solution proposed by FATIO could not be satisfactory in the long run. Our modern views concerning variation and mutation and concerning the value of statistics in the differentiation of various forms, as well as our views concerning the geographic isolation in the creation of new species in time simply had to prove their validity in the systematics of coregonine classification as well. Above all, much greater comparative series had to be made the subject of study.

ERICH WAGLER

WAGLER, E. "The Salmon-Like" (Salmonidae) II. Part, Coregonines. In "Handbuch der Binnenfischerei Mitteleuropas" ("Manual of Central European Inland Fisheries"), with statistical tables, 109 text illustrations, and 25 tables.

At the beginning of the thirties, the Bavarian ichthyologist, ERICH WAGLER, who repeatedly visited Switzerland, had the various corregonines of the different lakes shown to him, collected heads, counted gillrakers, and made measurements of body proportions. He also made inquiries concerning the views of our fishermen and was the author of several detailed studies. Finally he compiled his views in the "Handbuch der Binnenfischerei Mitteleuropas" ("Manual of Central European Inland Fisheries"). This study claims to reflect the present state of science, and in the eyes of the world it appears to be the coronation of decades of efforts. I must at this early point already emphasize that in this connection my own investigations, covering many years, have led me in entirely different directions. For this very reason I find it absolutely necessary to take this opportunity to reproduce WAGLER'S reasoning in somewhat greater detail and thus to characterize a period of ichthyology which, in my opinion, has led to dangerous false conclusions.

If we, first of all, summarize the quintessence of WAGLER'S thesis, then we can state:

In Central Europe there are four types of corregonines. They are best characterized in accordance with methods following those of MANGOLT and GESSNER. These basic forms have once upon a time arrived in our region in the course of their wanderings from the north, and have settled in our lakes. They are two "floating corregonines" and two "bottom corregonines".

TABULATED REVIEW BASED ON [illegible]ER

	"Blaufelchen" (Blue Corregonine)	"Gangfisch" (Wandering fish)	"Sandfelchen" (Sand corregonine)	"Kilch"
Rakethorns	narrow, long, numerous >30	narrow, long, numerous >30	broad, separated, shorter <30	broad, separated shorter <30
Head	pointed	pointed	blunt	blunt
Snout	more or less terminal	terminal or tends to be somewhat towards the lower side	more or less towards the lower side	very strongly on the lower side
Gill field	long, narrow, with parallel edges	long, narrow, with parallel edges	broader, shorter, edges diverging towards the rear	broader, shorter, edges diverging towards the rear
Back	blackish blue or bluish green	greenish, brownish green or olive-coloured	dark green to bluish green	brownish to olive-coloured
After death	slowly receding	rapidly receding	rapidly receding	rapidly receding
Fins	larger specimens sooty	only slightly sooty or not at all, white or slightly yellowish	somewhat sooty, especially in the case of larger specimens	white, no soot
Eye	small: 3-4% of length of body	large: 3.5%-4.7% of length of body	small: 2.8-3.8% of length of body	large: 4-5% of length of body.
Spawning grounds	mostly centre of lake above deep water	almost invariably the shore or shallow water	shallow water	depths
Colour of yolks of mature eggs	(?) orange	pale yellow, never orange	very light yellowish to almost colour-less	?
Rate of growth	rapid: at 4 years of age 30 cm and more	slow: after 4 years of age less than 30 cm. as a rule	rapid: at 4 years always more than 30 cm.	slow: at 4 years always less than 30 cm.

Nutrition	as a rule plankton and floating mosquito larvae	plankton, exceptionally sometimes also animals inhabiting the lake bottom: worms, mollusks, insect larvae	animals inhabiting the lake bottom: worms, mollusks, insect larvae, and in exceptional cases also plankton	almost exclusively animals inhabiting the bottom of the lake

1. Floating corregonine

(a) Large floating corregonine: "Blaufelchen" (Blue corregonine)

(b) Small floating corregonine: "Gangfisch" (Wandering fish)

2. Lake bottom corregonines

(a) Large bottom corregonine: "Sandfelchen" (Sand corregonine)

(b) Small bottom corregonine: "Kilch"

Added to this is the "kleine Märane" native in northern Europe exclusively, a floating marane whose snout is towards the upper edge.

Our many local varieties which the fishermen of the various lake regions have designated by numerous names, are all to be classified in accordance with this system so that there are lakes which contain all four, others which contain only three or two, and finally, also those which contain only a single form of corregonine. It would now be our task to examine the corregonine populations of the individual lakes in accordance with the norms established by the WAGLER differential diagnosis, and finally to determine whether any given lake contains one, two, three or all four types of corregonine.

WAGLER also arrived at this conclusion and has himself undertaken such a distribution.

The lakes of Switzerland have, according to WAGLER, the following corregonine populations:

	Blue Corregonine	Wandering Fish	Sand Corregonine	Kilch
666				
Lake Constance				
Lower Lake				
Lake of Walen				
Lake of Zurich				
Lake of Pfaffikon				
Lake of Greif				
Lake Baldeg				
Lake Sempach				
Hallwil Lake				
Zuger Lake				
Lake Lucerne				
Sarnen Lake				
Lake of Brienz				
Lake of Thun				
Lake of Biel				

Lake of Murten
Lake Neufchâtel
Lake Geneva

/ = present 0 = lacking ? = doubtful

The solution found by WAGLER is unbelievably simple. With a single blow all difficulties are cleared away, difficulties which, for centuries, have caused whole generations of researchers grave anxiety. If, however, we examine the details somewhat more closely, we soon become much less certain. WAGLER'S own confession concerning his all-encompassing work is also quite revealing:

"Individual specimens of coregonine are usually quite difficult to determine according to their external distinctive characteristics."

and

"For the outsider it is almost impossible to determine the individual specimens according to the available descriptions and keys and even a specialist frequently has quite a few difficulties in properly identifying specimens, if he is not acquainted with the locale in which they were found, and if he receives no data concerning the behaviour of the whole population."

Further on WAGER complains:

"The difficulty in determining is so great, because in the case of the vast majority of the species the distinguishing characteristics which would sharply divide them from each other have to date not been found. It is always necessary to take into account the sum of all physical properties. It is necessary to work with average or mean figures from series measurements and sometimes it is even necessary to use biological data."

WAGLER introduces his differential diagnosis (p.380) with the following modest remarks:

"At best, an attempt can be made to unite the most important physical properties of typical specimens and the biological characteristics of whole populations in an

overall table so that one may arrive at an opinion concerning the population after prolonged thorough observation."

Which specimens are "typical" and which characteristics or properties "important" is left to the subjective judgment of the investigator.

In connection with the table of p.124 we should, in the first place, note that it is "made to measure" for the types found in Lake Constance and that a coregonine of the other lakes only fits into this pattern with difficulty or not at all. We will attempt to prove this opinion in a subsequent part of our study. In any case, everyone attempting to work with this differential table will soon be severely disappointed. I, for my part, basing myself on such similar experiences in my study of 1939 could not refrain from accusing the WAGLER "system" ~~that it~~ attempts to squeeze and force a great variety of types into the four "species" constructed by him. This impression has been reinforced in the course of the last few years, and has led me to prepare this revision.

ODENWALL and BERG

In 1929 E. ODENWALL ("On the Classification of the various forms of Coregoni s. str. of northern Europe" Mem. Soc. fauna flora fennico - 1928/1929) again simplified the systematics of the Scandinavian coregonines by presupposing a single species in the process of differentiation. In this theory he was also joined by L.S. BERG who, in 1932, in his "Übersicht der Verbreitung der Susswasserfische Europas" (Review of the Distribution of Fresh-water Fish of Europe) only considers the Central European coregonine, Coregonus lavaretus L. as valid, and then goes on to divide it into "sub-species" and "nations". Alongside of this he claims that in northern Europe there is only the "kleine Marane" (small marane), Coregonus albula L., which, we must suppose, is to be subdivided in a manner similar to the one used in the case of with Coregonus lavaretus.

SUMMARY OF THE HISTORICAL PART AND INTERIM FINAL CONCLUSIONS

As is shown in the above historical outline of corregonine systematics, there have existed for a long, long time two basically opposite views. They could, perhaps, be called the "monophyletic" and the "polyphyletic" views. In the course of our own presentation we will go on to show that as a result of many long years of investigations, we have been increasingly forced to join the camp of the monophyletics. The reasons for doing so will be dealt with in greater detail in the next chapter of our study. Nevertheless, we would like to take one more opportunity to compile the arguments and counter-arguments presented by these two camps.

The polyphyleticians emphasize the very considerable differences between various types of corregonines: types with very slim, extended shape of body, on one hand, and short compressed bodies with high backs, on the other hand. They point out the difference in the size of eyes, the length of fins, the position of the snout either at the terminus or at the lower side, together with considerable differences in the shape of heads, a pointed, long snout component, on one hand, and a blunt short one on the other hand. Principally, however, they also point out significant physiological differences between the types; differences in habitat: such as the so-called "Schwebfelchen" ("floating corregonine") inhabiting the centres of lakes, the "Sandfelchen" ("sand corregonine") inhabiting shore waters, the "Grundfelchen" ("ground corregonine") living in the depths; they point out differences in nutrition with some types eating plankton while others prefer insects and mollusca, and others again flying insects and some, perhaps, even fish spawn. In addition to that they point out the difference in the rate of growth, the midget (small corregonine and the rapidly-growing large corregonine.

Great differences have also been proven to exist in the spawning habits: shore spawning, spawning at great depths, floating spawn, surface spawning in free lakes, and in addition to that, summer, fall, winter, and spring spawning. Considerable differences also appear in the rate of maturing. There are types which appear to mature as early as the second year, and others no earlier than the fourth year of their life.

The polyphyleticians found it unthinkable to unite in a single species forms having such considerable morphological and physiological differences. They considered it necessary to take certain type groups out of this total material and to establish differential diagnoses in order to draw the boundary line between these "species".

As a matter of fact, the real measurable differences between the coregonine forms are so great that using the standard of measurement applied to different parts of the system, it would appear justified to establish species diagnosis. It is also entirely feasible that during the post-glacial period, when the Alpine glaciers melted away and an extensive system of melt-water streams, water holes, ponds, and lakes, characterized the Central European landscape, several types of Scandinavian coregonines found their way into fresh water and thus were able to reach the sources of the streams. They could have, conceivably, also come into our regions subsequent to each other, that is to say, in different "pushes", but there are several factors which speak against this view. For one, it is difficult to suppose that there ever were so many Nordic types of coregonines to allow us to presuppose a special

Nordic species to be the ancestor of every single Central European special form of which, after all, dozens have been described. Thus, the presumption of the separate ancestry of our corregonine forms encounters one considerable difficulty: as we have already noticed, the Central European corregonine can clearly be divided into floating, shore and depth corregonines, etc., that is to say in accordance with their habitus and their habitat and they show physical characteristics which correspond to their environment. Now we are asked to believe that, for example, a floating type found in Lake Lucerne originates from a pelagic glacial sea-type and the deep lake corregonine from a specific inhabitant of the depths of the ocean, would it not appear much more reasonable to suppose that the differentiation among the corregonines only take place after their arrival in the heart of Europe, and that they all may well originate from a single ancestral type such as the one which we still encounter today in Siberian rivers as anadrome spawn wanderer. In the course of our presentation we will have to show that the monophyletic view can be supported by various additional arguments. At this point we would only like to emphasize three additional points:

(1) To this very day there is considerable lability among the corregonines. In very few decades the types have changed not inconsiderably and this is evident when we compare the data given by earlier authors with those given by FATIO or if we compare our present-day determinations with the measurements and descriptions made by FATIO.

(2) An overall review covering the physical characteristics and groups of characteristics of corregonines permits us to recognize a continuous uninterrupted magnitude of manifold varieties: we keep encountering intermediate forms and intermediate links.

(3) Even forms extremely different in their shape are sufficiently closely related that it is possible to cross them. So far as can be determined to date, such crossings in no way influence the fertility.

PREVIEW OF THE FUTURE SYSTEMATIC CLASSIFICATION OF THE CORREGONINES

From our historical review it appears that the systematics of corregonines are at present in what is nothing short of a chaotic state, and in any case that we are far removed from having sufficient clarity, which would allow non-experts to determine the boundaries separating the various categories of the system and to evaluate them according to their significance.

Under the circumstances, it appears that an entirely new system would be desirable. This can, however, not be achieved without radically removing all that has been done previously inasfar as it prevents objective research and to build anew on the ruins of what has been torn down. We must attempt to liberate ourselves from the old names and concepts and to look upon the object of our research, the

CENTRAL EUROPEAN CORREGONINE

with absolute objectivity as if we were dealing with, let us say, the European pike or cod, or also the grayling or the eel.

This object, the corregonine, is to be tested for the breadth (i.e. limits) of its variations and, in doing this, it must be attempted to find a mutual boundary (i.e. line of division) of the MODIFICABILITY, that is to say, the reaction to external environment on one hand, and, on the other hand, of the manifestation of genotypical differences. Only when we have achieved some measure of clarity in these basic questions, can we decide whether we are justified to divide the genus

Coregonus into several species, and whether we are entitled to evaluate the various partial populations as species or sub-species, or whether it would be more correct to speak of "local races" and "forms", that is to say, "nations" and "ecotypes".

In the special part of our study, which views the corregonine populations of each lake separately, we will not be able to avoid using the names of the "species" of earlier authors and we will -- insofar as this is possible -- attempt to delimit them (i.e. we will try to establish the boundaries separating them). But in doing this we must never forget that this does not constitute any testimony as to the real value of these systematic categories and we must wait to the very end before we can establish a system whose form will do justice to the present state of scientific knowledge.

Among the introductory problems which should also be discussed in this connection is that of the transplantation of alien corregonine stock into Swiss waters.

THE POSSIBLE INFLUENCES OF ALIEN CORREGONINES ON DOMESTIC STOCK

The question of whether, and to what degree the transplantation of alien corregonines (as alien corregonines transplanted to the seas of Switzerland we consider: 1. the American corregonine, Coregonus albus, the whitefish of North America; 2. the North European large marane, Coregonus marena Bloch. The large marane was brought to various Swiss lakes in considerable quantities during the year 1878-1885. This happened in Lake Constance, Lake Lucerne, 2,000 of them in Lago Maggiore, 17,000 in the Lake of Zurich, 46,000 in the Lakes of Lucerne, Sempach and Baldeg, 6,000 in the Lac de Joux. The amounts of whitefish transplanted in the years 1883-1886 were 25,000 into Lake Constance, 320,600 into Lake of Zurich, 206,000 into

Lake Lucerne, 43,700 into the Lakes of Sempach and Baldgg, 292,000 into the Lakes of Zug and Ageri, 160,000 into the Lake of Thun and Lake of Brienz. In addition to that, smaller amounts into the Lakes of the Lenzerheide, St. Moritz and into Lac de Joux, 81,860 into Lago Maggiore and 198,000 into Lake Geneva. Altogether somewhat over 1.3 million American corregonines were transplanted into lakes in our country), was able to influence our native stocks whether they remained pure or whether their blood became admixed with the later forms, or whether the combination of the two [illegible] new "races" -- all this is the subject of many divergent opinions, but one thing is certain: the most important transplantations of foreign corregonines took place some sixty years ago. Since that time no further significant transplantations have taken place. Throughout the epoch which has elapsed since then nothing whatever has been heard about the whitefish and nothing reliable concerning the German marane. Among the thousands of corregonines I have seen throughout the years, there was not a single one which, with any justification, could have been considered to be a whitefish or a "Madu-Märäne". Those which are called marane in the statistics of Lake Constance are, as WAGLER also emphasizes, highly problematical, because the fishermen tend to give the name "marane" to old fish of various types. Even the scientist, with his stricter standards, will, by the way, have difficulties to establish a reliable differential diagnosis between the Nordic marane and the Central European large corregonines.

Even if we were to suppose that all reports of marane received in the course of the last few decades referred to descendants of the Madu-Märane originally transplanted here, then the total result would be so insignificant that one would absolutely have to judge the

transplantation experiments as failures. THIENEMANN has calculated that the costs of all the transplantations amounted to approximately 14,000 marks. The value of all the catches throughout all the year at best approaches one half of the costs of transplantation. Under the circumstances, nobody can maintain that the invested capital has borne interest.

Another question is that of any possible racial influence of the domestic types through blood admixture with the aliens. If we calculate the destruction index on the same basis as we do for our native and properly acclimatized corregonines, then the number of descendants which could theoretically originate from the transplanted stocks of non-acclimatized aliens would be so small that one could hardly presuppose any influence upon the great domestic stocks. In this connection one should realize that a normal corregonine lake contains hundreds of millions of corregonine eggs every single year. ~~In this connection~~ it should be remembered that, for example, more than 30 million eggs which have been bred in artificial breeding plants are planted alone in the Lake of Biel. Of what help can the transplantation of several tens of thousands of alien breeding stock be? The probability that two of the rare aliens will meet again later on in the course of reproduction and produce purebred descendants is ~~mxxxxxpixxxxx~~ microscopically small. In addition to that, one must realize that the possibilities of survival for alien young fish are much worse unless some special hereditary characteristic has turned up which would have considerably increased the selection value of the new stock. Since, however, we have no facts supporting such a supposition, it appears justified to state that the influence caused by the transplantation of several litres of alien corregonine eggs during the 18th or the 19th

century can be ignored and that the present-day corregonine should simply be considered to be the descendants of our previous forms.

Naturally, what has been said above does not apply to the exchange actions covering whole decades which took place between the various lake regions of Switzerland, particularly in cases where the autochthonous populations were close to dying out, continued massive transplantations were able to change the picture. In this connection we particularly think of examples such as Sempach Lake and Hallwil Lake as well as Lake Geneva.

LIST OF THE COMMONLY USED TRIVIAL NAMES OF CORREGONINE TYPES IN SWITZERLAND

Before we publish the results of our observations we must still discuss the question of the TRIVIAL NAMES of the Swiss corregonine. Any such effort is connected with considerable difficulties since many once-common and well-known fish names have, in the meantime, disappeared. Modern times are also reflected in changes of language. An additional difficulty is that many of today's fishermen appear to be inferior observers when compared with their ancestors. Many a name which previously applied to a certain local form today indicates an entirely different kind than previously. In addition to that the last decade saw considerable and frequent transfers of eggs and spawning stock from lake to lake, and it became the habit to adopt the names of the "new" corregonines to those usually found in the locality to which they were transplanted.

First of all we will compile a list containing all corregonine names which have come to our knowledge.

Introductory Remark: The names in block letters are those still used today and they designate types which can be characterized fairly clearly. The names printed in italics are local names or locality designations lacking any other scientific foundation. The names reproduced in extended type refer to juvenile forms or immature specimens of known types. Collective names, as those used by the trade have recently become more common and they are printed in ordinary print. Obsolescent names are shown in parentheses. They are usually found in older literature but have disappeared from the contemporary language of fishermen.

(Adelfelchen)(nobility corregonine) - Lake Constance

(Adelfisch)(nobility fish) - Lake Constance

(Adelsperle)(nobility pearl) - Lake Constance

(Albele) - Lake Lucerne

ALBELI - Zuger Lake, Lake of Zurich, Lake Lucerne, Lake of Walen, Greifen Lake, Lake Pfaffikon

ALBOCK - Lake of Thun and Lake of Brienz

(Albule) - Lake Lucerne

(Albuli) - Lake of Zurich, Lake of Greifen, Pfaffikon Lake

(Balaie) - Lake of Biel

BALCHEN - Lake Constance, Zuger Lake, Lake Lucerne, Lake of Walen, Lake of Thun (Lake of Brienz?), Lake of Sempach

(Balch-Pfarrit) - Lake of Biel

BALDEGGER BALLEN - Baldegger Lake

BALLE or BALLEN - Hallwil Lake, Lake of Thun, Lake Brienz, Zuger Lake, Lake Lucerne, Lake Sempach

(Besole) - Lake Geneva (?), perhaps only in Lac de Bourget

(Bezola) - Lake Geneva, perhaps only in Lac de Bourget

(Bezoule) - Lake Geneva, perhaps only in Lac de Bourget

(Bisole) - Lake Geneva, perhaps only in Lac de Bourget

BLAALIG - Lake of Zurich

(Blablig) - Walen Lake

BLAULIG or BLALIG (Blue One) - Lake of Zurich.

BLAULING (Blue One) - Zuger Lake

BLAUFELCHEN (Blue Coregonine) - Lake Constance

(Blauligbratfisch)("Blue Frying Fish") - Lake of Zurich

(Blauling) (Blue One) - Lake of Zurich, Lake of Wallen

(Blawlig) - Lake of Zurich

Bodenblaalig (Bottom Blue One) - Lake of Zurich

BONDELLE or Bondèle - Lake Neufchapel (Lake of Biel?)

(Brater) ("Fryer") - Lake of Biel

(Bratfisch) ("Frying Fish") - Lake Zurich

BRIENZLIG - Lake of Brienz

(Buchfisch) - Lake of Thun

(Edelbalchen) - Lake of Thun, Lake of Brienz, Lake Lucerne, Zuger Lake

EDELFISCH (Noble Fish) - Lake Lucerne

Felsenblaalig ("Rock Blue") - Lake of Zurich

FERA - Lake Geneva, Lake Neufchâpel

Féra blanche - Lake Geneva

Féra bleue - Lake Geneva

Féra jaune - Lake Geneva

Féra noire - Lake Geneva

Féra petite - Lake Geneva, Lake Neufchâpel, Lake of Murten

Féra du Travers - Lake Geneva

Féra verte - Lake Geneva

(Férit) - Lake of Murten

(Ferra) - Lake Geneva

GANGFISCH ("Wandering Fish") - Lake Constance

(Gibbion) - Lake Neufchâpel

GRAVENCHE - Lake Geneva

GREIFENSEEALBELI - Greifen Lake

Grundern - Lake of Walen

(Hagling) - Lake of Zurich

HALLWILER BALLEN - Hallwil Lake

(Heglig or Haglig) - Lake of Zurich

(Hegling) - Lake of Zurich

Heuerling (This Year's Fish) - Lake Constance

Hürling - Lake Constance

KILCH - Lake Constance

(Kirchfisch)(Church Fish) - Lake Constance

Krautbalchen (Herb Fish) - Lake of Thun, Lake of Brienz, Lake Lucerne, Zuger Lake

KROPFER ("Adam's Apple") - Lake of Thun, Murten Lake

(Kropfelchen)(Adam's Apple Coregonine) - Lake Constance

(Kropflein) (Small Adam's Apple) - Lake of Thun

(Lavaret) - Lake Geneva

Meidel - Lake Constance

Midelfisch - Lake Constance

Miesaeler - Lake Constance

PALCHEN - Lake of Biel

PALEE - Lake Neufchâtel, Lake of Murten (Lake of Biel?)

Palée de bord - Lake Neufchâtel

Palée blanche - Lake Neufchâtel

Palée de fond - Lake Neufchâtel

Palée noire - Lake Neufchâtel

Palée petite - Lake Neufchâtel

PFAFFIKONERALBELI - Pfaffikon Lake

(Pfarrig) - Lake of Biel, Lake of Murten

(Pfarrit) - Lake of Murten

(Pferrig or Pferrit) - Lake of Murten

Renken - Lake Constance

SANDFELCHEN (Sand Coregonine) - Lake Constance and others

Schwebblaalig (Floating Blue One) - Lake of Zurich

Schweber (Floater) - Wallen Lake

(Schweinbalchen) - Lake of Thun, Lake of Brienz, Lake Lucerne, Zuger Lake

Seelen (Soles) - Lake Constance

SEMPACHER BALLEN - Lake of Sempach

Silberfelchen (Silver Coregonines) - a somewhat nebulous term especially on Lake Constance.

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SOMMERALBELI (Summer Whitefish) - Lake Lucerne, Wallen Lake

Spiezlig (Pointed One) - Lake of Thun

Spitzlig (Pointed One) - Lake of Thun

Steinbalchen (Stone Whitefish) - Lake of Thun, Lake of Brienz, Lake Lucerne, Zuger Lake

Stuben or Stuben - Lake Constance

WALENSEEALBELI - Lake of Walen

Weissfelchen (White Coregonine) - Lower part of Lake Constance, occasionally still used but frequently misunderstood.

WEISSFISCH (Whitefish) - Lake Lucerne, more recently replaced by "Albeli" but still used occasionally.

Weissgangfisch (White Wandering Fish) - Lake Constance

WINTERALBELI (Winter Whitefish) - Lake Lucerne, Lake of Walen

(Zugeralbock) - Zuger Lake

The term "Felchen" (Coregonine) by itself is used to designate the various types in waters more recently populated by coregonines: Lake Ageri, Lungern Lake, Klon Valley Lake, the term "Coregoni" is used to designate the coregonines of the Tessin who have their origin in the stock of the northern Swiss lakes.

Occasionally especially large sand coregonines are called "Maranen". This name even appears in statistical tables but no proof has been established that the large specimens are anything else but old sand coregonines. (see also p.130 of German text).

For an even more detailed characterization, we give below an overall compilation of the most important trivial names, together with the spawning periods and spawning locations as they were rallied at the time of V. FATIO, some fifty years ago.

LOCAL VERNACULAR NAMES CURRENT IN SWITZERLAND AT THE TIME OF FATIO TOGETHER WITH THE TIMES AND PLACES OF SPAWNING COMPILED BY LAKES

Vernacular names	Spawning Time	Place
Lake Constance		

Sandfelchen (Sand Coregonine)	November	shore
Weissfelchen (White ")	"	Sloping bottom, shore
Blaufelchen (Blue ")	November-December	" "
Kilch	Oct.-Nov.	At great depths
Gangfisch (Wandering fish)	Nov.-Dec.	At depths - half depths
Lake of Zurich		
Bratfisch (Frying fish)	Nov.-Dec.	Half depths
Blaulig (Blue One)	Nov.-Dec.	Half depths
Albeli	December	Depths
Hagling	?	?
Walen Lake		
Felchen (Coregonine)	Nov.-Dec.	Half depths
Pfaffikon Lake		
Albeli	November	Half depths
Greifen Lake		
Albeli	November-December	Half depths
Lake Lucerne		
Balchen	Nov.-Dec.	Shore - rocks
Edelfisch (Noble fish)	August	At greath depths
Weissfisch (Whitefish)	Jul.-Oct.	Half depths
Zuger Lake		
Balchen	September	Shore, rocks
Albock	Sept.-Oct.	Great depths
Albeli	?October	Depths
Lake of Brienz		
Balchen	Nov.-Dec.	Shore - rocks
Albock	September	At great depths
Brienzlig	October	Half depths
Lake of Thun		
Balchen	December	Shore - rocks
Albock	September	At great depths
Kropfer (Adam's Apple)	Aug.-Sept.	Depths
Lake of Sempach		
Ballen	Nov.-Dec.	Half depths

Baldegger Lake		
Ballen	Nov.-Dec.	Shore - sand
Hallwiler Lake		
Ballen	Nov.-Dec.	Shore - rocks
Murten Lake		
Palée	Dec.-Jan.	Sloping bottom
Pfarrig	Dec.-Jan.	" " , depths
Kropfer (Adam's Apple)	Dec.-Jan.	" "
Lake Neufchâpel		
Palée de bord	November	Shore - rocks
Palée de fond	Jan.-Feb.	Sloping bottom, depths
Petite Palée	?December	Half depths
Bondelle	January	At great depths
Lake of Biel		
Palchen	September	Shore
Balch-Pfarrit	?	?
Pfarrit	Dec.-Jan.	Depths
Lake Geneva		
Féra	Feb.-Mar.	Great depths
Gravenche	December	Shore, sand

Today, after about 50 years, some of the names have disappeared. Others have changed in their meaning. On Lake Constance today the Sandfelchen (sand coregonine), Weissfelchen (White coregonine) and Kilche are usually designated as "Silberfelchen" (silver coregonine) to differentiate them from the "Blaufelchen" ("Blue coregonine"). Young silver coregonines of Lake Constance are called "Gangfische" ("Wandering Fish"). Many fishermen are not quite clear concerning the exact characteristics identifying the lower lake Gangfische ("Wandering Fish").

It becomes quite apparent that the fishermen, if for no other reasons but for practical ones, and in part motivated by commercial factors, are working towards the differentiation of the various "types". They are familiar with the spawning and catching grounds for the individual types and they know

when and where the various types can be caught, for it is part of their trade to know as much as possible concerning all these details. In view of this, the fishermen used to, and, to a certain extent, still continue to give the young fish different names than the older ones of one and the same type. We also know of cases where the local variety of coregonines of a certain lake region is, by tradition, considered to be particularly tasty and is preferred over those imported from the other lakes. It frequently even brings a premium on the market. There have even been instances of cases being brought to court when, for example, a fisherman designated a type of fish caught in Lake Constance with a vernacular name of his home region as if the domestic fish had some sort of "trade-mark copyrights". For all these reasons it is understandable that scientific research required the clarification of these confused concepts and its replacement by an orderly system.

In the historical part we have shown that to date all attempts have failed and that the confusion has, if anything, been increased by the appearance of the systematicians. This on one hand is unfortunate, but on the other hand it is entirely understandable in view of the fact that the genus Coregonus appears to have so great a variability that it can be considered to be unmatched by any other genus.

Before we go on to prove this in detail it may be well to explain the natural history of the coregonines in its more general aspects.

GENERAL PART

NATURAL HISTORY OF THE GENUS COREGONUS

Belonging as they do to the "narrow-snout types" among the salmonides, the genus Coregonus together with the Thymallus form a sub-family of the Salme and in the main

they differ from the grayling in that they have a relatively small rear fin. Their snout is equipped with very weak non-permanent teeth, the position of which will be discussed in greater detail later on, while the teeth of the grayling snout are more constant.

The genus was first designated by ARTEDI. The name refers to the shape of the pupil which is not circular or round, but comes to a point in the front.

VON SIEBOLD gives the following diagnosis of the genus:

"The narrow snout with very fine non-permanent teeth or entirely toothless. Body somewhat compressed laterally. Medium-sized scales fall out easily. The rear fin starts just in front of the belly fin. The leading edge of the rear fin is longer than its base."

The most important vernacular names commonly used in Europe are:

Gallic countries:	Féra
German-speaking Switzerland:	Felchen
Austria:	Rheinanke, also Reinanke
Southern Germany:	Renke
Northern Germany:	Marane

In particular the different types are given many different vernacular names which, in the case of Switzerland, we have compiled in another part of this study (see p.132, German text).

Illustrations - p.137

Fig. 2 - Shore Albock, compressed type, Merligen, on Lake Thun.

Fig. 3 - Pfarrig from the Lake of Biel. Intermediate type.

Fig. 4 - Albeli inhabiting the depths of Lake Walen. This specimen shows juvenile proportions, large head, large eye, slimness and light-coloured fins.

Fig. 5 - Albock - Milters from Lake Thun, simultaneously caught near Merligen in a spawning ground. The longer

one is somewhat lighter than the shorter one. Fully mature with spawning marks.

Upper: Length: 39 cm.; Circumference: 18.6 cm. Weight: 420 g.
No. of scales: 86; No. of gill rakers: 31

Lower: Length: 36.5 cm.; Circumference: 21.6 cm.; Weight: 500 g.
No. of scales: 78; No. of gill rakers: 33

This picture shows that body proportions are an unreliable indication for the differentiation of so-called "types".

THE EXTERNAL APPEARANCE OF COREGONINES

The Scales

The head is invariably free of scales; the first rows of scales are to be found at the shoulder level; the size is scales is variable. A unit of measurement is to be found in the number of perforated scales located on the "side-line", (The variation limits being approximately 70-100). At the root of the tail fin there are numerous tiny scales which often extend far beyond the base of the fin rays.

The Shape of the Body

The shape of the body varies very considerably and leads to the differentiation between slim "floating coregonines" and more compressed high back "bottom coregonines". Between these two extremes ~~there~~ are all imaginable intermediate stages to be found. These proprtions can be measured with the aid of the "slimness coefficient" (length divided by circumference). The juvenile specimens are, in the main, slim while the elder specimens appear more compressed (see figs. 2-4).

The Fins

The back fins start approximately at the centre of the body just behind the point of the greatest circumference. The upper edge slopes sharply because the foremost fin rays are considerably longer than the real ones.

The fat fin is small and is located approximately half-way between the back and the tail fin. It is light grey to black in colouring.

The tail fin appears to have a deep incision. Its concaveness (see Fig. 6) varies from type to type. Often the two parts are uneven ("heterocercia") with the lower tail surface tending to be larger than the upper one (see Fig. 7).

The anal fin is relatively small. Its rear edge is slightly concave. Position: immediately behind the anal aperture.

The breast fin is approximately as long as the head and the belly fin somewhat shorter.

While the non-paired fins of the back and the tail become pigmented at an early date, the anal fin and the paired fins remain white in the juvenile state and only become covered with soot with the approach of sexual maturity. This particularly applies to the male specimens. "Overpointing" (acromegalia) may appear in older specimens and is caused by the forward fin rays growing more profusely. This becomes apparent on the back fin and the belly fin and occasionally also on the breast fins and is indicative of certain types, while this phenomenon in other sub-populations is the exception rather than the rule.

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Fig. 6 - Concaveness of the tail fin, a characteristic strongly influenced by age in salmonidae.

Fig. 7 - Tail fin of a "Weissfelchen" (White coregonine) of the lower part of Lake Constance. The appearance of heterocercia is quite frequent in all ecotypes, including blue coregonines and especially in bottom coregonines. In certain years it may affect up to 50% of the fish population of any lake.

The Head

In older specimens the head is relatively small. In juvenile ones it is larger. Four types maintain their juvenile proportions throughout. When viewed from the side

the difference in the point of the head and the position of the mouth becomes apparent: pointed and stubby snout, mouth at the end, at the lower edge or, infrequently, at the upper edge. A typical sideview is shown in Fig. 8, fairly large, flat upper jaw, more or less at a slant depending upon the position of the mouth (see Fig. 9).

The "Jaw Area"

The "jaw area", the shape of which is ascribed so much importance by E. WAGLER, can best be seen from below (see Fig. 10). The 'Radii branchiostegi' can be recognized and alongside of them the edge lines of the lower jaw. In the small-headed types these lines tend to be more or less parallel, while they converge more strongly towards the front in the broad-headed types. In evaluating this characteristic care must, however, be taken to determine whether the animal examined is bloated or not.

The Teeth

Frequently hardly any trace of teeth can be established. In juvenile specimens teeth are placed on the jaw, but they soon break off. The tiny teeth near the pharynx and the root of the tongue usually remain, but they are frequently so minute that they do not protrude from the mucous membrane and therefore they cannot be seen, but only felt.

Illustrations p.140

Fig. 8 - Various head profiles and mouth positions: mouth at the upper edge, mouth at the end, mouth at the lower edge. Chin more or less protruding.

Fig. 9 - Types of heads. Top: Floating coregonine type ('Gangfisch')

Bottom: Bottom type coregonine ('Kropfer')

THE GILL-RAKER APPARATUS

Very characteristic and significant for the differentiation of the various types is the gill basket with the tiny gill-raker teeth, the density and length of which may vary considerably from type to type. Generally speaking, it can be said that the farther out a fish population lives in the regions of free water, the more numerous and minute the gill-raker teeth will be found (Fig. 11). More recent research which, unfortunately, had not been completed at the time this monograph was published has enabled us to use the minute structure of the gill-raker teeth as a characteristic indication of certain inter-relationships. In the living fish, the thorns are covered by a mucous membrane which tends to swell up immediately after death and then disintegrates. If the gill-rakers of a no longer entirely fresh fish are cleansed in rapidly running water, then the cartilage core on which the tiny secondary teeth are located becomes visible. This cartilage core consists of many different lamella-like structures, some of which run lengthways while other tend to run crossways, as well as ring-shaped cartilages which appear to be the location of the roots of the tiny secondary teeth (Fig. 12). It has already been determined that types which were previously considered members of one and the same "species" such as the Kropfer of Lake Thun and the Kilch of Lake Constance in fact showed great differences in the minute structure of the gill raker teeth, while, on the other hand, representatives of one and the same "nation" had certain recognizable similarities in the basic pattern of their minute structure. Unfortunately the investigation of this relationship has to date not reached a stage at which we would be entitled to make a more detailed positive statement.

The Eye

The most noticeable part of the eye is the shape of the pupilla, the forward edge of which is, as already mentioned, drawn out to an angle. The iris is silver coloured and occasionally its upper half is slightly darkened.

Spawning Exanthem and Spawning Products

The spawning period is accompanied by a noticeable spawning exanthem on the flank. It takes the form of cartilage-like rows of papilla on the scales. The number and size of these warts is considerably greater in male specimens than it is in females.

The fertility of the genus Coregonus is very considerable. The spawning products are frequently produced in very great quantities. Thus SCHILLINGER has on one occasion counted no less than 20,700 eggs produced by a single blue coregonine weighing 490 g. On an average, this means that we can count on 3,000 eggs per 100 g. of body weight. The dwarf coregonines even produce more than 4,000 eggs per 100 g. of body weight. This results in the spawners being usually strongly swollen with the approach of the spawning season.

In its internal organization the genus shows very close similarity to the other salmonidae. The great number of appendices pyloricae which tend to become attached to the duodenum is worthy of notice.

Illustrations p.142 and 143

Fig. 10 - Jaw field: the length-breadth relationship a:b used by Italian researchers.

Fig. 11 - Gill rakers at the first arch. All from coregonines originating from the Lower Lake. The illustration shows the great variability in number, thickness and length of teeth.

THE LIVING HABITS OF THE COREGONINES

Wanderings and Swarm Formation

It appears that basically the coregonines originally were anadromous river-wanderers like the other salmonidae. In many lakes they have to this very day maintained certain definite features characteristic of wandering fish. WAGLER, however, claims in his writings that this "wanderlust", this "old salmonidae heritage" was, in the course of his investigation, "invariably found to be very modest in its extent". On the other hand, it must be emphasized that coregonines are occasionally caught in all of Switzerland's larger rivers (the Aare, the Reuss, the Limmat) and in the Rhine as far down as Basel and, according to WALDNERS report, even as far as Strassburg and, according to LEUTHNER, even at Speyer, and the fact that great spawning columns move from the Lake of Biel to Lake Neufchatel and from there on to Lake Murten. Enormous wandering columns of Albocks from Lake Thun were recently found to be in a section of the river Aare between the lakes of Thun and Brienz. It has also been found that at certain water levels coregonines from Lake Alpnach rise into Sarner Lake and it is well known that whole swarms of ascending coregonines, some of whom actually spawn in the flowing water, can be caught in the Linth Canal (between the Upper Lake of Lake Zurich and Walen Lake). It is also well known that the Gangfische (wandering fish) is frequently found in the flowing waters of the Rhine between Constance and the Lower Lake. KLUNZINGER (1892) reported that the "Gangfische" are found in swarms on the "Rhine between Constance and Ermatingen, particularly in the shallow water with sandy bottom, the Lower Lake Gangfische ascending, and the Gangfische from Lake Constance descending, both of them evidently following their 'longing' for flowing water."

But even the tribes whose present-day living habits keep them in still waters, very often undertake extensive wanderings. In contrast to the opinions expressed in BREHM's "Animal Life" where it is maintained that "the wanderings exist only for the purpose of reproduction, but not in search of better nutrition." we must maintain that at certain times, particularly in spring, coregonines come from ~~far away~~ very distant locations to certain feeding grounds. Thus, for example, they tend to collect in the Lucerne arm of Lake Lucerne in order to devour the masses of chironomid pupae which rise from the bottom, and this, in turn, results in anglers often getting astoundingly big catches, particularly of small coregonines (Albeli). The same applies to Lake Thun where great swarms of coregonines "pasture" near Spiez and Faulensee. It would, without doubt, be possible to state many similar instances from other lakes. In Ageri Lake and Zuger Lake there also appear to be mass wanderings in the direction of favourable feeding grounds. The fact that the same fish undertake new mile-long voyages when their old pastures are beginning to fail, or when the sexual drive makes itself felt, is supported by numerous unintentional markings. In Lake Lucerne Albeli can be caught with hook and line only near the town of Lucerne and the fine hooks not infrequently get caught in the jaws of the little fish, although the latter may liberate themselves. Thus these fish can be recognized after many months. Such fish with fine fishhooks were, however, not only caught near Gersau, but frequently also near Brunnen and even as far as Fluelen. This means that they wander approximately 40 and even more kilometres upstream only to return once again to their starting point later on.

A similar process evidently also takes place with the large floating coregonines, the "Edelfische" (Noble Fish) which, in winter-time, are caught in the Lower Lake but in summer even far beyond the Urn Basin.

Illustration p.144

Fig. 12 - The minute structure of several gill rakers: 1 Ballen from Lake Hallwil; 2 Kilch; 3 Kropfer (Adam's Apple), of Lake Thun.

Major dislocations have also been ascertained in the case of the blue coregonines of Lake Constance, AUERBACH, MAERKER, SCHMALZ and NUMANN have followed these wanderings more closely:

"In spring the blue coregonines are first caught in the upper part of the lake between Langenargen and Rorschach only to move on to the central parts of the lake between Friedrichshafen and Romanshorn and also between Immenstaad, Hagnau and Uttwil and Guttingen later on. In July and August our fishermen usually set their nets at the exit of the lake between Meersburg and Munsterlingen. At this time they also visit the Constance "funnel" and the "Uberling Lake", the latter almost to its very end. From September onwards the fishermen again turn more towards the main lake between Hagnau and Immenstaad and the last catches are usually made once again in the upper regions of the lake."

The fishermen are firmly convinced that the blue coregonine actually wanders in a corresponding pattern. We have, incidentally, received similar reports from Wurm Lake and Atter Lake as well. The influence of subsurface currents, plankton distribution, and other circumstances on this wandering phenomenon is still not quite clear to us. One thing, however, is certain; that in addition to the horizontal wanderings, vertical wanderings also take place. We have fairly good information concerning this in the case of Lake Lucerne, Lake Geneva and Lake Neufchâtel. The blue coregonines of Lake Constance assemble in the quadrilateral Langenargen-Friedrichshafen-Romanshorn-Rorschach shortly before the spawning time just under the surface of the water and far away from the shore.

On the other hand, the "Balchen", i.e. the large bottom coregonines, seek the shallowest shore locations during their spawning period and occasionally they come to within a few decimetres from the rocky shore, while in summer they tend to live at a greater distance from the shore and at considerably greater depths. The "depth coregonines" (Kilch) of Lake Constance and the tribe of the "depth Albock" ("Kropfer") of Lake Thun also approach the shoreline at certain times. SURBECK (1916) reports Kilchs being caught by floating nets at depths of 9 metres. I, for my part, have obtained Kropfer caught at depths of 5 metres in Lake Thun. This indicates that even these tribes which appear to have become completely acclimatized to still waters are capable of making considerable vertical wanderings. WAGLER also reports:

"The 'wanderlust' is not even completely surpressed in the Kilchs but the distances are covered in one and the same body of water and mainly in the vertical direction."

In order to clearly understand these wanderings and their biological significance it is important to note that the coregonines wander in swarms. The tendency towards swarm formation is deeply rooted in this salmonidae genus and it makes its appearance in the very earliest breeding stages. The dissociation and association of coregonines will have to be covered in greater detail later on. At this time it should only be noted that the coregonines in their collective wanderings take certain routes which differ for the various tribes and, inasfar as it can be judged to date, there is a strange sense of "memory orientation" which leads individual swarms of fish to certain specific spawning grounds which evidently have been theirs for generations. Even though the general validity of this rule has not been proven by marking experiments, it can be considered to have been established

that certain tribes, for example, of Lake Lucerne, invariably arrive at certain places at a certain time. This "loyalty to a location" is no longer considered to be as mystical and unique as it was in the past. Let us just remember the herrings, the eel, the salmon, and the lake trout, all of which, without doubt, have a "homing instinct", but we still do not know the means and markings which the swarms use for orientation. Very probably the fish allow themselves to be directed by seasonal, periodic phenomena to which they have learned to react by their inherited race memory -- specific method of reaction which, perhaps, has been developed by biological selection. We must never forget that in every swarm formation there appears certain supra-individual reaction characteristics which cannot be deducted from the psychological makeup of the individual animal but which make the swarm appear as a higher biological unit governed by its own rules.

As a result of our studies of coregonines we have arrived at certain conclusions concerning the original beginnings of swarm formation and the prospective significance of the association problem and we would now like to discuss them with reference to an interim publication (STEINMANN, P., Über die Schwarmbildung bei Felchen, - Concerning the Swarm Formations by Coregonines- Rev. suisse Zool. 53 - 1946).

We have bred coregonines from the egg stage to the completion of the fourth year of life, and to the beginning of sexual maturity, in breeding establishments which were put at our disposal. First these were aquaria, later larger, deeper, concrete "ponds". In this connection we were able to make a number of interesting observations concerning the

formation of swarms. As early as the very first days of their life, the tiny fish form swarms composed of thousands of individuals which keep moving around day and night, in darkness and in light, without stopping, and which, later on, also stick together as "age-group swarms". We have reason to believe, also, that coregonines in free nature stick together in similar societies. The whole art of the floating net fishermen is to set a suitable net of the proper gauge in the suitable subsurface stream so that a swarm of wandering coregonines swims into it. But also the anglers with their tiny hooks who frequently pull up one apparently identical coregonine after the other, at one and the same feeding ground, know that they have a small tribe swarm dancing around their fish-hook. A few metres further on nothing can be caught and the swarm in the depth can also move from one moment to the next so that an angling ground which was most profitable suddenly becomes quite bare. These small tribal swarms consist of age groups and occasionally they unite in large mass columns which can even be seen from ships, provided they swim close to the surface. The significance of these swarms is not quite clear in all respects. Certainly, nutritional, psychological questions must be taken into consideration: fish seek those layers of the water in which the plankton tends to increase, or in bays in which the mud on the bottom allows hundreds of thousands of chironomide pupae to rise to their metamorphosis, or the underwater "lawn pastures" found in shallow places where the pisidii and snails live, but the formula "wandering from an exhausted to a plentiful pasture place" is certainly not the entire solution of the problem. It is illogical why such a change of locale, if it appears necessary cannot be made by individuals

or small groups rather than giant swarms.

In the past, as we have noted above, the problem of wandering swarms has simply been connected with the question of spawning. As a matter of fact, in many cases the beginning of spawning maturity appears to result in a particularly close link between individuals and a trend towards more active wandering. It is natural that the eggs must be deposited in a location where the young fish spawned from them will have the best possible chance of survival. If pastures and feeding grounds of the parents cannot offer these conditions, then a change in locality would appear desirable and the instincts towards such a change have a selection value. In this connection let us remember the salmon, which feeds in far-off regions of the ocean but, at the beginning of the spawning type, each seeks its native river mouth and then, without stopping, moves from the ocean to the very edge of the Alps where the young fish will find a suitable environment for growing. In order to achieve this, such collective methods as the formation of swarms and wandering columns become necessary since the success of the spawning depends upon the fishes arriving at the spawning place not singly, but in spawning communities.

But this still by no means credibly explains the accumulation of thousands and tens of thousands of fish. Equally it is difficult to understand why the swarms already meet months or even years preceding the spawning period.

We will still have to discuss the prospective significance of the wandering swarms in connection with the type differentiation -- as an isolation mechanism -- in conclusion we would only like to establish once more: the coregonine biology is, to a high degree, characterized

by the phenomenon by the collective wandering. A complete biological study of these fishes as individuals is not possible. They must rather be studied as members of the swarm, just as the bee's actions and habits can only be understood by studying its position in the bee society. The coregonine swarm is an "organism" subject to certain rules of behaviour. Special motives govern its actions, and these motives cannot be deducted from the deeds of the individual, but only from the supra-individual collective interest.

NUTRITION

The fact that a great proportion of our coregonines knows how to catch masses of plankton crusts is certain. Frequently lumps having the size of a nut or occasionally even a hen's egg can be found in the fishes' stomachs. These lumps consist exclusively of Bosmina coregoni or Bythotrephes longimanus. Occasionally Daphnia, Cyclops, Heteracope and Diaptomus are also consumed in mass quantities and it appears that individuals are capable of "picking" certain species from among the available plankton organisms. The "floating coregonines" which are caught in floating nets, i.e. those which have pastured in the free water regions, are, during the summer months, exclusively or at least almost exclusively plankton eaters. Infrequently there are remnants of flying insects found in the stomachs. They probably were blown by the wind from the shore onto the surface of the water, but there are also partial swarms who inhabit greater depths, particularly in the oligotrophous lakes on the bottom of which there still exsits an abundant fauna. This particularly applies to older coregonines which consume lake-bottom nourishment during summer. Generally it can be said that in springtime almost all coregonines keep to bottom nutrition and that,

in addition to that, there are partial populations which only occasionally and temporarily become plankton eaters. Nevertheless, we can agree with WAGLER and other authors who have found that the stomachs of the so-called "floating coregonines" mostly contain plankton and remnants of flying insects while the "bottom coregonines" contain mostly nourishment found at the lake bottom and only infrequently plankton.

In the course of our breeding experiments which covered three consecutive years, we arrived at the belief that even very obvious floating coregonines start eating nourishment from the bottom (dew-worms and limnae) relatively early, that they attempt to snap wasps and ants which may be on the surface of the water, and that they show great dexterity in catching mosquito and other dipteral larvae.

Most important among the crustacean plankton consumed by the floating coregonines, we as a rule find the cladocera (Daphnia longispina, Bosmina coregoni, Leptodora and Bythotrephes). The dwarf coregonines having long gill raker teeth such as the "Albeli" "Brienzlig" etc. occasionally rely upon a Bythotrephes diet almost exclusively. In shallower waters we have, however, also been able to observe tribal swarms whose members have apparently specialized themselves on mosquito larvae. As we have already previously mentioned, the rising of the chironomide pupae from the bottom of the lake to the surface causes some swarms of coregonines to concentrate en masse in the regions where this takes place (Lake Thun, Lake Lucerne, etc.). On Hallwil Lake we had the occasion to open coregonine stomachs which contained a lump consisting of Corethra larvae, a fact which, by the way, has also been reported by WAGLER concerning the blue coregonines of Lake Constance.

The latter -- and this probably also applies to the large floating coregonines of the other lakes according to data known for a number of years maintain themselves for long periods throughout the summer and early autumn on a fish diet, and in doing so they not infrequently eat their own offspring (see Fig. 13). On some occasions juvenile coregonines measuring up to 5-6 cm. in length were found in the stomachs of coregonines . FREY-BAUMGARTNER once caught a blue coregonine whose stomach contained no less than 47 young perches measuring from 3-4 cm. in length. Even coregonines of medium size weighing approximately 250 g. and up, tend to become predatory. FREY over a period of a whole year conducted a series of stomach investigations, taking a proximately 100 samples per month. He tabulated his results in the following "feeding calendar":

January	:	mosquito larvae and some plankton
February	:	empty
March	:	?
April	:	? (mostly empty)
May	:	33% plankton, remainder empty
June	:	all filled with plankton
July	:	all filled with young perches
August	:	ditto
September	:	ditto
October	:	part filled with plankton, part filled with perches
November	:	the small coregonines full of plankton, the large ones with perches having a length of up to 6 cm.
December	:	mostly empty (spawning period).

The coregonines caught near the shore at lesser depths, particularly those tribes which, in their appearance, were similar to the description of "sand coregonines" often had their stomachs filled with algae or black leave-compost in addition to that pisidii, snails, chironomides and worms. In such locations coregonines can be most successfully caught with bottom fish-hooks which

are best baited with dew-worms (Klontal Lake and others).

Illustration on p.151

Fig. 13 -- Contents of the stomach of a blue coregonine from Lake Constance: young perches, July 1949.

Sphaeriidae and water mites are also found in stomachs of coregonines of Lake Thun as well as Lake Constance. During the spawning period, the coregonines are busy eating eggs and occasionally a tribe that is not spawning at the time visits the spawning grounds of another and uses them as a pasture until it has practically exhausted it. Thus, for example, various authors have reported that the "kilch" of Lake Constance becomes a major consumer of spawn during the spawning period of the blue coregonines. In this connection we would also like to draw the reader's attention to the frequent mention of this phenomenon in the relevant literature (SURBECK 1925, 1928, 1931; ZANDT 1928; BIRRER and SCHWEIZER 1935) as well as the relevant passages from WAGLER'S Works and his summary in the Manual of Inland Fisheries. We, for our part, would like to record our experiences as follows:

All coregonine tribes are capable of consuming both plankton and nutritional matter found at the bottom, both in deep and shallow parts of the lake. They also do not overlook somewhat larger bits such as dew worms and small fish. They change their dietary habits with their age, the time of year, and their habitat. Some of the partial populations tend to prefer plankton, others nutrients found on the lake bottom. But none of them limit themselves to any one of these categories.

It is particularly noticeable that in lakes which are approaching eutrophication extremely fat specimens of coregonines are caught (Hallwil Lake, Zuger Lake, Lake Zurich, Lake of Biel), but that these tribes are by no means particularly rapid growers. It frequently happens

that dwarf coregonines with an unusually thick layer of fat are caught while on the other hand it is not infrequent that even in summer large types of coregonines show digestive tracts which are very poor in fats. This fact clearly indicates that growht is not only determined by the amount of available nutrition but also by hereditary factors. The next section will deal with this in greater detail.

We have to raise various objection to the practice of WAGLER who, among other things, also uses the dietary habits in order to aid him in the diagnosis of the differences separating his four coregonine "types". While it is true that the coregonines caught in summer with floating nets are, in the main, plankton eaters, it must be considered that, if at the same time, bottom nets were used, then without doubt we would also find tribes which, in their exterior appearance, seem to belong among the floating coregonines who have, however, consumed a mixed diet. On Lake Thun we have frequently observed that entirely different types were all feeding chironomides, so to say next to each other, in one and the same feeding ground. The coregonine types usually found at great depths, that is to say, those whose stomachs normally contain principally pisidii, can occasionally grow quite fat on plankton. This, according to WAGLER'S own observations, also applies to the Kilch of Lake Constance. The fact that blue coregonines switch over to lake bottom nutrition is evident from some specimens I caught in the lower lake in 1947. Thus, if the biological characteristic "dietary habit" is used to aid in the differentiation of "types" of coregonines, then very particular care must be taken, for, in this respect, coregonines are by no means constant and the rules established from time to time cannot be relied upon.

GROWTH

In various publications, WAGLER has pointed out that the "rate of growth" is an excellent differentiation characteristic between the various coregonine types. Indeed, he has called it "perhaps the only method allowing us to differentiate between the types, provided the available specimens are of sufficient quantity".

We cannot by any means associate ourselves with this view. We must, rather, emphasize the very contrary, namely that the rate of growth of various coregonines shows a great fluctuation from lake to lake and from tribe to tribe and that even the rate of growth within a single tribe and the same body of water changes considerably over a period of years (Figs. 14 and 15). In subsequent sections we will explain our opinion with the aid of examples, and at this point we would only like to state several theoretical objections against WAGLER'S concept.

The size achieved by an individual specimen at a certain age -- let us say after two years -- depends upon its hereditary growth tendencies but also and equally upon its individual development environment, its individual fate which, perhaps, enabled him to bring in a particularly rich harvest on a good feeding ground, or, on the other hand, may have caused him particular nutritional difficulties. In the artificial breeding of young coregonines in ponds it has been determined that every swarm contains fast and slow growers. Sooner or later some coregonines become the victims of parasites who slow down the rate of growth. Cold spells in spring also tend to bring delays in growth. Particularly great influence upon the rate of growth is caused by the direct competitors for food, i.e. the fellow-members of the swarm. One task which, from the very beginning, must be considered as hopeless is any attempt

to deduce any of the genotypical GROWTH FACTORS from the phenotypical SIZE MEASUREMENTS. Just imagine: from the chaos of coregonine forms among which it is quite impossible to find a differentiation based on shape characteristics, we are supposed to be able to determine the species purely on the basis of the rate of growth, provided the age of the specimen is definitely known!

WAGLER himself knows only too well how difficult the age determination based on scales frequently is. I, for my part, take a very sceptical view of his explanations concerning "intermediate rings", which should not be counted when determining the age, because they may have been influenced by changes in nutrition, habitat or temperature during the summer, and thus may "masquerade" as "winter rings", although the detailed explanation made by NUMANN and others concerning the intermediate ring problem are most enlightening, I nevertheless found the individual cases occurring in actual practice invariably most doubtful. This particularly applies to forms which inhabit the depths and certain floating populations of unstable character. Where no other solution is possible, it is simply necessary to admit that a given scale is uncertain and open to differing interpretations. The fact that WAGLER practically bases the whole of his "specific" growth phenomenon exclusively on studies of scales is, in my opinion, wrong for various reasons:

1. I too have examined many hundreds of scales. In the course of this I have noted over and over again, that coregonines of the same age-group frequently have very different scale patterns. Sometimes the central field is large and the additional rows which have grown later are narrow, and at other times the reverse is the case. (Illustration 16).

2. Very often I find in places where one would have to expect narrow winter rings merely a very narrow zone which shows certain irregularities in the overlapping of the rings. I am in possession of extensive material of this type of scales, and from it I conclude that at times of nutritional deficiency (starvation) the growth of scales not only ceases entirely but that the outermost edge produced during the summer may tend to disappear again. This without consideration of the rings, so that two, three and even more rings may be attacked at an agle. The new spring rings then appear at the irregular edges and they, that is the spring rings, again show a concentric pattern (Illustration 17).

3. In older specimens in particular the broad "spawning marks" are encountered. They also indicate the presence of periodic reduction phenomena at the edge of the scale. (Illustrations 18, 19).

4. The width of the rings at various radii of the scales is very uneven and the number of rings also frequently does not correspond equally in all directions. (Illustration 16).

5. The growth of the scales, as EINSELLE has convincingly demonstrated in 1943, is more rapid in the oral direction than in the caudal one.

Illustrations on page 156 of the German text.

Illustration 16 -- Two-year-old "Gangfisch" broad inner rings.
Two-year-old "Gangfisch" narrow inner rings.

Illustration 17 -- Discordant sclerites. Detail from a "spawn mark" area. It is evident that before the formation of new rings took place strong and far-reaching erosions occurred. Walen Lake Albeli, three years old, 21 cm., 73 g.

Illustration 18 -- Four-year-old Albeli with spawn mark from Walen Lake.

Five-year-old coregonine with two spawn marks.

Under the circumstances I cannot see how one can reconstruct the rate of growth from the growing zones of a coregonine scale. No matter how surprisingly elegant the DAHL-LEA method is, and no matter how convincing SEEGERSTRAALE's explanation may be, a prerequisite for the practical applicability for the "indirect method of measurement" would be a strictly proportional rate of growth of fish and scales. This may be the case in certain fishes, but these prerequisites do not exist in the case of coregonines. The rate of growth curves of coregonines must, in my opinion, therefore must not be based on scale patterns but they can only be achieved by direct measurements in the course of the statistical tabulation of which there must be a complete elimination of all those individual specimens whose age cannot be determined with absolute certainty on the basis of their scales.

Before recording our own figures we must still critically compare the WAGLER tables whose calculatory basic principles we fundamentally refute:

First Year of Age

"Rate of growth of blue coregonines" (Table 34): Differences ranging from 7.2 cm. (Mond Lake) to 13.1 cm. (Alp Lake) and 13.3 cm. (Sims Lake).

"Rate of growth of Gangfische" (Table 35): Differences ranging from 7.7 cm. (Lake Chiem) and 11.7 cm. (Lake Lucerne)

"Rate of growth of the 'Sand coregonine'" (Table 36): Differences ranging from 10 cm. (Lake Walen) to 11.3 cm. (Sempach Lake).

"Rate of growth of 'Kilche" (Table 37): Differences ranging from 8.4 cm. (Lake of Thun) to 10.3 cm. (Ammer Lake).

We, for our part, really cannot recognize anything

"specific" in these first year rates of growht. If, in addition to this, we realize that, for example, the "Gangfische" of Lake Lucerne, the well-known "Weissfischli" (White fish) or "Albeli" are, in part, summer spawners and in part winter spawners, then, to say the least, the question must be raised whether these various tribes can have a similar typical growth pattern or whether the biological differences would not find some sort of expression in the scale patterns.

Second Year of Age

Even at the end of the second year it is not possible to note very "typical":

"Blaufelchen" (Blue coregonines) from 16.3 cm. (Lake Chiem) to 23.3 cm. (Baldeg Lake)

"Gangfisch" from 15.0 cm. (Lake Chiem) to 19.8 cm. (Kochel Lake)

"Kilch" from 16.7 cm. (Lake Constance) to 16.8 cm. (Lake of Thun)

"Sandfelchen" (Sand coregonines) 21.7 cm. (Lake Constance) to 25.7 cm. (Sempach Lake).

Third Year of Age

A greater degree of agreement in the average size only begins to make its appearance with the third year, but there, average of the "Sandfelchen" (Sand coregonine) is somwhere close to the average of individual "Blaufelchen" (Blue coregonine) and the size of the "Kilch" falls within the range of the "Gangfische".

"Blaufelchen" from 25.7 cm. (Lake Chiem) to 30.1 cm. (Baldeg Lake)

"Sandfelchen" from 31.3 cm. (Lake Constance) to 33.8 cm. (Zurich Lake)

"Gangfische" from 20.1 cm. (Lake of Walen) to 25.4 cm. (Laach Lake)

"Kilche" from 19.9 cm. (Ammer Lake) to 22.0 cm. (Lake Constance).

In this connection it should be noted that these average lengths of individual populations have not been obtained through direct measurement of the fish in question, but by means of calculation of the growth zones of the scales and, further, that only the average figures thus calculated but not the range of variation and distribution were figured out. An example of the errors inherent in this type of backwards calculation based on scales is shown by the already altered study made by EINSELE. He had the occasion to investigate a considerable number of "Grossrenken" aged 1 and 2 summers respectively (1941). Rather than obtaining a length of 8.7 cm. for the fish of one summer, as could be expected according to the WAGLER method, he obtained mean values of 17.5 cm. and the average weight of the little fish was not 4 g. as it would have had to be according to WAGLER's calculations, but rather 40 g. Another typical feature was the very great difference in the rate of growth among various members of this age group, the smaller members of which measured 7 cm. while the largest measured 20.3 cm. and the heaviest individuals had no less than sixfold the weight of the lightest.

Thus, no further proof will be required to show that, for a clear distinction and diagnosis of coregonine types this "sole" characteristic of rate of growth is useless.

We have attempted to investigate material at our disposal not by the study of annual scale rings but by direct measurements of the growth of the fish itself and in the course of a parallel experiment conducted over a period of five years under identical breeding conditions

we have followed the growth of a "dwarf" tribe and a rapidly growing "race". In the special part of our study we will publish several graphic representations and tables indicating the growth relations of several populations. Presently we will limit ourselves to one example, namely that of Lake Constance (see table on p.159 of the German text).

Our figures, when compared to those in WAGLERS tables, show considerable deviations from the latter. Perhaps some of the differences are due to the fact that the "fishing net selection" caused me to miss certain size categories in individual catches. I definitely know that in evaluating this statistical material it becomes apparent that certain age groups are caught in unequal quantities as a result of certain net gauges (net sizes).Because of this not much reliance can be placed upon the exact number of individual specimens caught but I was not particularly concerned with the numbers of individual specimens in the various size classes but merely with the possible variation breadth. This, as is apparent from our table, is quite large enough to indicate the difficulties encountered in any attempt to use rate of growth figures for a characterization of "species".

The reader's attention should also be drawn to several additional features which make WAGLERS rate of growth figures appear particularly suspect:

Up until now it was well known that Baldeg Lake was inhabited by a tribe of coregonines somewhat below average size. In WAGLERS tables it, however, marches at the head of the large-size "Blaufelchen" (blue coregonines). We may well ask ourselves whether this is due to the fact that perhaps the investigation took place in a year having unusually favourable growth conditions?

From WAGLERS' tables it also becomes apparent that from some lakes the author had only fairly sparse material at his disposal. Thus, for example, only nine specimens of the "Sandfelchen" (sand coregonine) of Lake Zurich and only fifteen from Sempach Lake. In order to make any really valid evaluation of the growth conditions of a tribe, it would be necessary to have at one's disposal various age groups and a much more extensive collection of material covering a period of years. This evidently was not the case in WAGLERS' investigations.

One additional circumstance apparent from a study of WAGLERS' tables appears particularly doubtful to me. It would have been reasonable to expect that the genotypical basis of the rate of growth would be particularly expressed in the first years of life, but it is during that very period that the greatest differences between the rate of growth of coregonines of different lakes appear, a phenomenon which indicates anything but a genetic uniformity of the "species".

Our own direct measurements, together with age determination, also clearly emphasize the lack of constancy in the growth conditions of various tribes. We have not only compared our figures with WAGLERS' mean values but also with what has been recorded by FATIO. Unfortunately FATIO only gives the extreme limits for "grown-up" coregonines, and then he usually does so only in the case of the "old ones". The mean value calculated on this basis is only conditionally comparable. Nevertheless, it can be established that without doubt the rate of growth of coregonines in various lakes today shows considerable differences from the state of affairs some fifty years ago.

We will select only a few examples from our materials and for comparative purposes we will also draw upon the studies conducted by BIRRER and SCHWEIZER concerning the coregonines of Lake Lucerne. As far as possible, the measurements of fish immediately upon first reaching maturity have been considered.

TABLE (p.161 - German text)

	FATIO	WAGLER	BIRRER and SCHWEIZER	MY OWN
Hallwill Lake, Lake Lucerne ("Weissfischli") (Little White Fish)				
Lake Thun ("Brienzlig")				
Lake Bienne and Lake Murten (Pfarrig)				

It becomes evident that in certain lakes the average weight of a certain age group appears to have increased, while in others it has decreased. In different cases we established that the fish's average size increases when the numbers decrease. This can, for practical purposes, be considered a rule. We find a parallel development in the case of numerous other fish. According to the testimony of fishermen of the lower part of Lake Constance, the "Gangfische" there are said to have increased in size ever since they appeared in less dense swarms than they did previously.

At this time we do not intend to discuss this phenomenon in greater detail. We would merely like to point out that two possible reasons for the increase in size with the decrease of swarm density can be taken into consideration:

1. The competition for food among members of the same swarm.
2. The anxiety (nervousness) of the individual fish who have to swim in too dense a swarm which may interfere with its feeding.

These cases certainly bear testimony against WAGLER'S thesis of the uniformity of the rate of growth and of the possibility of characterizing the "species" by their growth.

In addition we must also realize that in various tribes we were able to establish quite extraordinary individual differences in growth, a fact which finds no expression in WAGLER'S tables which only take mean values into consideration.

SURBECK, in 1928, has established the following limit values for the length within certain age groups of "Gangfische": (table p.162 German text):

Age years	Body length

We know of similar limit values in the case of other tribes. The "Sandfelchen" ("Sand coregonines") showed very considerable individual differences in the rate of growth: (second table p.162 German text):

Age years	Body length

Thus it appears that a 7-year-old fish was smaller than a three-year-old of the same species! In the size group of the 40 cm. long fish there were 4, 5, 6, and 7 year old ones! If we were to ask ourselves what causes these noticeable differences in size, particularly in the

"Sandfelchen" then we cannot help but take the varying nutritional conditions in the litoral zone into consideration. The nutritional conditions of the coregonines of a certain stretch of shoreline will vary with the character of the shore, its flora, and density of the perch population as well as that of other competitors.

If various year groups of a tribe of one and the same lake are compared, then not infrequently noticeable differences can be established. Climatic conditions, the date of the awakening of nature in spring, water levels, pollutions, all have varying effects in different years.

But very considerable differences in size can also appear among coregonines inhabiting different regions of one and the same lake basin. In 1931 SURBECK compared the "Gangfisch" of the Upper Lake with those of the Lower Lake of Lake Constance and established that there were considerable differences between the two partial populations. We, for our part, have noticed the relationship existing between the density and the rate of growth in Lake Thun. It is interesting to note that the two "Schwebfelchen" ("floating coregonine") types of the Lake which can be clearly differentiated from each other indicate some sort of antagonism which was first observed and reported by the fisherman HURLIMANN and subsequently confirmed by me. For a period of years the number of the large floating coregonines of the Lake, the "Albocke", had been decreasing considerably. At the same time the average size decreased considerably. Simultaneously the small coregonines, called "Brienzlig", who, in the main, also feed on plankton, increased in number and became noticeably smaller. After a period of several years, a reversal of this process began taking place. One could note an increase in the number of "Albock" and at the same time a decrease in the average weight of these large

coregonines. The reversal in trend may have been favoured by the prevailing fishing practices.

The fact that the swarm density by itself -- that is to say even without the competition of other coregonine tribes -- influences the rate of growth of coregonines is supported by the finding that during so-called bad years, that is to say, years when, during the spawning and subsequent breeding periods, extremely unfavourable climatic conditions prevail or when the majority of juvenile coregonines do not survive because of some natural catastrophe, the surviving coregonines tend to have above average dimensions.

There are certain indications that quantitatively considerable stocks of predatory fish have an unfavourable effect upon the rate of growth of the coregonines of a certain lake. Evidently the cause in such a case must be sought in the constant anxiety (nervousness) of the coregonine swarms resulting from the actions of hunting pikes, trout and larger perches. Here again anxiety tends to interfere with growth.

We must further consider one additional growth factor which, in our opinion, is one of the most important and the genotypical basis of which is clearly established by our experiments: the "maturing age", i.e. the typical degree of early or late maturity for the different tribes. As long as the fish still has entirely undeveloped gonads, everything it consumes can be utilized for the growth of its body, but as soon as the gonads begin swelling, a large, perhaps an even overwhelming part of the nutrition is utilized for the production of reproductory cells. This stage is also characterized by an enlargement of the blood vessels nourishing the gonads. In addition to this the development of the spawn pupillae and the more intensive

wanderings which precede the spawning act bring about a great consumption of nutrients. On the other hand, it is quite common in the salmonidae family to stop feeding immediately before the spawning period and even to interrupt the consumption of food for several weeks. While only mature coregonines participate in this starvation, immature ones continue feeding and thus obtain a considerable head-start in growth. The tribes whose members already start spawning in the second and third year of life thus have a relatively small increase in growth, contrasting to this is the tendency of the late spawners to reach giant proportions because they pass through four or five years of growth before their gonads mature. We will return to this relationships in the chapter dealing with reproduction, and on this occasion we would merely like to note once more that the age of maturity which varies considerably from tribe to tribe can, to a very great degree, influence the rate of growth. It is probable that in this process the antagonistic effect of various hormones play a certain role so that the development of the maturity hormones which adapt the body for sexual activities suppress the creation of growth hormones. The hereditary difference of types then would be connected with this "equilibrium mechanism".

We cannot conclude our chapter dealing with the rate of growth of coregonines without pointing out two circumstances the influence of which is disputed and questionable. They are the degree of eutrophication of the waters of the lake, on one hand, and the "space factor" on the other hand.

As we have already pointed out in the section dealing with nutrition there are frequently obese small

coregonines and thin large coregonines. As a matter of fact, it is by no means true that bodies of water containing abundant nutrition invariably contain well grown specimens or that oligotrophic bodies of water containing little plankton are inhabited by particularly small coregonines. In this connection we would merely remind the reader that, for example, the Lungern Lake, a dam lake offering little nutrition and having a low temperature, is inhabited by larger coregonines than the Sarner Lake which, although it contains an abundance of flora and plankton, is inhabited by "Felchli" who, in spite of an excellent constitution, have an unfavourable rate of growth until the stocks were replenished by the transfer of tribes having a better rate of growth. From that moment onwards the Sarner Lake was also inhabited by coregonines having a favourable rate of growth. Thus the degree of eutrophication of a body of water is by no means an indication of the rate of growth of the coregonines inhabiting it. We could cite several additional examples similar to the above.

Inasfar as the "space factor" is concerned, we would like to point out that the rule "the greater the body of water, the greater the fish" is not universally valid. If we review our measurements in this respect, then we are forced to conclude that the coregonines in the sub-alpine lakes do not follow this rule, While it is true that the "Féras" of a large lake like Lake Geneva grow quite rapidly, as do the "Sandfelchen" (sand coregonines) of Lake Constance and Lake Lucerne, the very same Lake Constance is also inhabited by the small "Gangfisch" and Lake Lucerne by the dwarf coregonine "Weissfischli",

while, on the other hand, small lakes such as Ageri Lake and Lungern Lake produce good-size coregonines, the dimensions of the coregonines found in the small Baldegg Lake are greater than those of the "Hallwilerballen" who inhabit a much more extensive body of water. It is also true that the coregonines of the small lakes in the central part of the Canton of Zurich tend to grow rapidly while in large lakes, like Lake Brienz, contains minute coregonines -- the genuine "Brienzlig" -- in all these cases the "space factor" appears to play no role whatever. This, by the way, also applies to coregonine lakes outside of Switzerland and is clearly evident from WAGLER'S extensive compilations. Merely as an example we would like to cite the case of Sims Lake, a small body of water which produces rapidly-growing coregonines, and, as a counter-example, Ammer Lake a good-size body of water whose "Kilch" invariably remains small.

Our investigations into the growth of various coregonine tribes together with the results of previous investigations lead us to the following summary conclusion:

1. Without doubt the "growth tendency", that is to say, the hereditary inclination to grow, is quite different in various tribes. We are, however, able to judge the actual "growth" only, which is a product of both this inherited tendency or inclination and environmental factors.

2. It is impossible to group the tribes into "species" according to their rates of growth. In individual lakes there are, for example, the "Kleinfelchen" ("small coregonines") which have a tendency to dwarf development, while in other lakes they reach the dimensions of "Grossfelchen" ("large coregonines"). The latter are, however, also not uniform in their rate of growth. Their maturing age is frequently the deciding factor

in these differences among individual tribes.

3. The fact that the effective growth to a great degree is co-dependent upon environmental factors adds an element of difficulty to any effort to differentiate between the "species" according to their rate of growth, so that measurement of individual year and age groups cannot be relied upon for purposes of species diagnosis. Such measurements are just as much a reflection of the development conditions under which a fish operation has lived as they are an indication of the genetic basis of growth. These development conditions include not only the amount of available nutrition but also the temperature, climatic conditions, as well as the competition for food (this includes competition by other members of the same swarm -- swarm density), anxiety caused by the presence of predatory fish and other factors.

REPRODUCTION

The Matury Age

(Age at the Beginning of Puberty)

The coregonines -- in common with the other Salmonidae in general -- have a relatively short period of adolescence. They mature at an early age. Too little notice has been given to this circumstance in the past. A prerequisite for the study of the maturing age is the possession of incontestable age determination, the technique of which has only been recently perfected and, if possible, breeding experiments for the controlling of the observations made in nature.

We know today that there are coregonines who mature as early as the end of their second year of life. On the other hand there is evidence supporting the assumption that certain tribes only reach their sexual maturity in the fourth and even in the fifth year of their lives.

WAGLER has illuminated this relationship in the case of the blue coregonines and the "Gangfisch" of Lake Constance, and he emphasizes that it appears to be a peculiarity of small coregonines to mature earlier than large coregonines. Thus, some Gangfisch actually achieve maturity in their second and the remainder in their third year, blue coregonines infrequently in their third year, majority in their fourth year, and some only in their fifth year. For our part we can confirm WAGLER'S opinion. It is not only valid for Lake Constance, but also for the other coregonine lakes. I, however, draw somewhat different conclusions from these facts than WAGLER has done.

The facts established in our own investigations dealing with the early and late maturing of coregonine tribes are based in part on breeding experiments from egg to the stage of puberty and, in part, on age investigation of the scales of coregonines which had reached spawning maturity.

We will publish the results of the breeding experiments at Arth further on and on this occasion we merely want to establish that the fish bred from the eggs of the "Albeli" (a small type coregonine from Lake Alpnach) produced mature milters at the end of the second year, while the fish bred from Féra eggs under exactly identical breeding conditions were still immature at the end of the third year with some of them reaching maturity only during the fifth year.

Over a period of years we were able to find mature specimens among the "Weissfischli" (Albeli) of Lake Lucerne which were but two years old. Other examples of early maturity are the "Brienzlig" and the "Albeli" of Lake Walen. Among the "Brienzlig" the small coregonines

of Lake Thun, we encountered numerous two-year-old specimens of both sexes which had achieved entire sexual maturity. Most of them measured from 18 to 20 cm. We did not establish the percentage of two-year-old ones in the total catch because the "net selection" which WAGLER justly considers a source of error would, in any case, have resulted in misleading figures. In the autumn of 1935 we set some extra dense nets coming from Lake Brienz in Lake Thun and the result was a catch of a considerable number of mature dwarf coregonines which, in that size category was quite unknown to the local fishermen. They were two-year-old "Brienzlig" during the first spawning period mostly in sizes under 20 cm.

Recently we were also able to observe similar conditions in Lake Constance. During the spawning season of the Gangfisch in the winter of 1949-50 we were able to convince ourselves that the fixed nets which were used with such success in the spawning grounds above Ermatingen were quite ineffectual in catching the early spawning Gangfische at Ermatingen. On the other hand, fishermen using draw nets caught a considerable number of small "Gangfische" because the "drawn" mesh of the nets frequently prevented the small fish from escaping. In years previous to this I have been able to obtain considerable numbers of two-year-old male specimens by this method. The catches of December , 1949, also resulted in a bountiful supply of female specimens of the 19-21 cm. size category. They were all fully matured. Their egg supplies accounted for up to 25% of their body weight. They were, in the main, two-year-old specimens. It is typical that the largest among the small coregonines, namely those having body lengths from 21 to 23 cm. are three-year-olds and

a clearly noticeable spawning mark can be found on their scales. These fish could be differentiated from the two-year-old ones having almost exactly the same size at the first glance, because the point of their belly fin was blackened. The three-year-old fish who spawned for the first time were much larger. They and the four-year-old ones dominate in spawning catches and usually reach a weight of 160-180 g. They are the ones which are usually caught by fishermen using set nets and present-day "Gangfische" breeding depends in the main on these and older age groups. The dwarfed two and three-year-old Gangfische if caught at all are usually smoked without being first slit open and are thus eliminated from artificial breeding. Insofar as these dwarf fish spawn in free nature, their potential offspring is constantly endangered by water pollution and spawn-eating enemies. Thus they are at a disadvantage when compared to the three-year-old ones who have spawned for the first time not only at Ermatingen but probably also in other locations, for the three-year-old "first spawners"have the full benefit of artificial breeding. Probably the circumstances discussed above are, in the main, responsible for the increase in the average size of Gangfische which has been reported by fishermen.

In view of the significance of all these questions it should be pointed out that the figures compiled on page 171 of the German text tend to emphasize the fertility of early spawning tribes. We can thus quite definitely establish that coregonines which have spawned early show a poor rate of growth in subsequent years.

Exactly the opposite applies for "late spawners". We have received five-year-old "first spawners" of the "Blaalig" variety, the bottom coregonine of Lake Zurich,

which weighed around 700 g. These fish, which were made available to us through the kind attention of Mr. STUDER, a fisheries supervisor, had scales with remarkably large growth rings for the first three years of their lives. Evidently their late maturity exercised a particularly favourable influence on their rate of growth. The same applies to the corregonines of Lake Geneva (Féras), those of Lake Neuchatel (Palées) as well as those of Langen Lake (Coregoni). I am sure that the "Sandfelchen" (sand corregonines) of Lake Constance can also be included in this category. But the number of age determinations established to date is too small and probably also too uncertain, thus preventing us at present from definitely including the "Sandfelchen" (Sand corregonines) in the group of lake maturing corregonines. Nevertheless we would like to refer to SURBECK'S study who, in 1916, investigated 54 sand corregonines of the spawning period 1915 and found among them no less than 28 five-year-old ones and 13 six-year-old ones, while the younger and older age groups were only weakly represented. BIRRER and SCHWEIZER in 1938 also found that the five-year-old specimens were prevailing in a series of spawning fish ("Balchen") of Lake Lucerne. In the course of the years 1948 and 1949, we have in vain attempted to find any corregonines spawning near the shoreline which were younger than five years. This investigation was conducted in Lake Lucerne, Lake Constance and Wallen Lake and repeated in 1950 in Lake Bienne.

Between the early and late spawning types there are those forms which have moved their main spawning period towards the end of the third year. These tribes also have a rate of growth between that of the early maturing and the late maturing types. Thus there is a clear relationship between the maturing age and the rate of growth of

corregonines, a relationship which, like every other rule, perhaps also has certain exceptions but which, on the whole, appears to have a definite validity.

In order to illuminate the differences in concept, the following should perhaps also be noted:

WAGLER on page 51 of his study, "Der Bestand an Blaufelchen usw." ("The Blue Corregonine Stocks, etc.") writes: "It must be noted that the slow growing corregonines tend to mature early and the more rapidly growing ones tend to mature late." We are of the opinion that the maturing age is the primary cause, the "rate of growth", the effect, that is to say: not early maturity of small corregonines and late maturity of large corregonines, but rather a tendency for the early maturing types to remain small and the late maturing types to grow large.

This directly leads to an important principle for the corregonine economy: if we desire to aid the economically valuable corregonines of a lake, then we must attempt to decimate the early maturing types by authorizing the use of suitably narrow-meshed nets. This is best achieved by fishing during the spawning period in the spawning grounds. We will return to this problem in the section dealing with the management of corregonine lakes.

It is only natural for those who do this work in practice to know the differences between a slowly growing early mature type and a young "large corregonine". The most accurate method of doing this is the examination of the gonads. The fish desiring to spawn in a given year are already noticeable early in summer, but scale-pattern is also very helpful in most cases. Young large corregonines have "growth strips" composed of numerous rings and mostly they also produce normal rings in winter. The small corregonines, on the other hand, produce only few rings in

the course of the summer months, and in the place of winter rings we frequently merely find "seams" which indicate that the outer zones formed in the summer have in part eroded during the winter, so that the lines tend to converge. In addition to that a "spawning mark" in the form of a broad protruding ring is frequently found in three and four-year-old specimens.

A DIFFERENTIATION OF THE SEXES

Generally speaking, the males and females are very difficult to differentiate during the year. In the course of the maturing of the gonads, the somewhat more rounded females are more easily recognizable. They are usually also somewhat lighter in pigmentation, particularly on the fins, and in addition to that their "spawning exzema" is less developed than that of the males. During the stage of full maturity we can add the following characteristics: an outward rounding out of the sex papilla which tends to acquire a reddish colouring which also persists for a certain period after spawning, while the male, even during full maturity, has a light coloured anal region. Generally speaking, the sex of large corregonines can be more easily distinguished than that of small corregonines. After spawning the skin papillae of the "spawning exzema" rapidly disappear.

The question has been raised whether the intensity of the spawning exzema which, for example, manifests itself in the number of papilla rows can be used in establishing a differentiation between races. We have gained the impression that there are considerable individual differences in this respect and that one and the same individual specimen may behave differently in subsequent spawning periods. We have been able to establish this in the course of our own breeding experiments during which we brought males to maturity in two years in a row.

THE INTENSITY OF FERTILITY: WEIGHT OF GONADS, NUMBER AND SIZE OF EGGS

We have at our disposal random samples giving the weights of the gonads of most of our corregonines and we also have records of random observations concerning the size of their eggs. These findings on the whole correspond to those recorded by WAGLER, BIRRER and SCHWEIZER, as well as SURBECK and others.

The frequently surprising fertility of the smaller and smallest corregonine tribes is particularly noteworth. The following are some figures indicating the number of eggs per kilogram of body weight as recorded in various publications:

"Sandfelchen" (Sand corregonines) of Lake Constances --	13,000 - 18,000
"Balchen" of Lake Lucerne	12,000
"Blaufelchen" (Blue Corregonines) of Lake Constance	3,000
"Albeli" of Lake Lucerne	41,000

We have ourselves frequently weighed the ovaries of mature females and compared their weight with that of the whole fish. In doing this one must, of course, limit one's investigations only to specimens which are about to spawn. In order to demonstrate the reproductive capacity of dwarf corregonines, we have extracted certain data from our tables. We have purposely limited ourselves to fully matured specimens and will not include any data which may refer to immature specimens or those which have already started spawning.

Table on p.171 of the German text

Weight of roe of several small corregonines expressed in terms of percentage of total body weight:

1. Walen Lake ("Albeli")

Length	Weight	Weight of roe	Per cent

2. Lake of Brienz ("Brienzlig")

3. Lake of Thun ("Brienzlig")

4. "Lower Lake" ("Gangfische")

We are thus able to confirm that the small corregonines develop relatively larger gonads than the large corregonines. We have been able to establish this for both spawners and milters, basing ourselves on observations made in Lake Thun, Sarner Lake, Lake Lucerne and Walen Lake. The "Bondelles" of Lake Neuchâtel also develop relatively reproductive organs when compared to the "Palées" which grow to a considerably larger size. All this leads us to conclude that the "small corregonines" are more fertile than the "large corregonines". In order to be able to evaluate these relationships correctly it would, however, be necessary to know whether the size of the gonads is the same in young and old spawning fish in those who spawn for the first time and those which have already spawned several times. We are still lacking accurate data concerning this. We have, however, repeatedly seen over-age specimens of spawning corregonines whose gonads were very sparsely developed. In Lake Thun we even encountered quite definitely senile specimens with stunted gonads.

THE EGGS

In his"Manual of Inland Fisheries" WAGLER has combined a great deal of material concerning the colour, size, weight and specific gravity, as well as the "sinking speed" of corregonine eggs. We have but little information of our own to contribute, and would only like to note that the conditions are subject to considerable fluctuation from lake to lake, from tribe to tribe, and even from one individual to another. I came to this conclusion on the basis of random samplings made in conjunction with the investigation of larger series of spawning fish.

As far as the colour of the eggs is concerned, we must definitely refute the concept that it is in any way specific as to species or race. The fact that the individual spawning swarms have differing nutritional habits during the summer months has already been established in the section dealing with nutrition. The uniformity of egg colour of a spawning swarm hardly signifies anything else but a preceding period of similar nutrition. Members of one and the same type of corregonine who differ only in their living habits may have eggs of quite different colours. I have also noted that in the course of stripping larger quantities of corregonine spawners, one may encounter individual specimens having lighter or more reddish eggs than the average. These may be outsiders who may have joined the swarm at a later date.

Insofar as the colour of the eggs is concerned, it is necessary carefully to sift the available published results of measurements very carefully because of the different measuring methods used by the various authors, and also because the age of the eggs measured, and thus the degree of swelling of the egg-shells very evidently do not agree in the different measurements.

We can confirm one fact on the basis of our own experience: as a rule larger fish have larger eggs, but even this statement only applies conditionally. Particularly in the case of small corregonines who spawn several years in succession it was found that older specimens, even though they may have remained small in size, develop larger eggs. Yes, even larger ones than first spawners of larger size tribes do. BIRRER and SCHWEIZER, in the course of measuring the diameter of Albeli eggs of Lake Lucerne, found that it varied from 1.88-2.3 mm. and arrived at a mean of 2.11 mm. In comparison the "Balchen" of Lake Lucerne have considerably larger eggs: they vary from 2.71-3.23 mm.; mean 2.98 mm. According to the results reported by WAGLER and ELSTER, the blue corregonine eggs are somewhere in between: they vary from 2.4-3.0 mm.; mean 2.4 mm. On the other hand, the eggs of the "Gangfisch" are relatively large -- even though this fish must be counted among the small corregonines. According to WAGLER, they vary from 2.4-3.5 mm.; the mean amounting to 2.82 mm., thus greater than that of the blue corregonines. This high figure in the case of the "Gangfisch" probably is due to the fact that the spawning swarms of Gangfisch contained considerably numbers of older fish who, as is the habit with all Salmonidae, develop relatively large eggs.

While conducting an investigation dealing with a spawn of "Gangfelchen" (wandering corregonines) and "Sandfelchen" (sand corregonines) near Ermatingen on the Lower Lake during the winter 1949/50, I took particular note of females of the Gangfisch variety of various ages all of whom had reached spawning maturity. I was able to establish that the smaller females/who were but two years old had in fact produced eggs which were clearly smaller in size than those produced by the larger older fish. In this connection I would merely like to draw attention to the fact that the presently available data concerning the "size of the Gangfisch egg" as published in

available literature should be treated very critically. A great deal depends on individual circumstances and such figures, no matter how carefully they were compiled and calculated, still cannot by any means be considered to have universal validity.

SPAWNING PERIOD, BEGINNING, DURATION

Generally speaking, the corregonines are considered to be winter spawners. Most of them do, in fact, conduct their spawning activities during late autumn and early winter, but there are remarkable exceptions. We know of some very definite summer spawners inhabiting the lakes of Switzerland. WAGLER also reports that the "Kilch" of Ammer Lake has a spawning period extending from June right into August. The "Edelfisch" of Lake Lucerne spawns from July into September. The "Kropfer" and the "Brienzlig" of Lake Thun as well as the Brienzlig of Lake Brienz spawn in late summer. The same applies to certain spawning swarms of Lake Lucerne and Walen Lake ("Sommeralbeli"). Lake Zurich at one time also had a small corregonine spawning in summer and infrequently it is still found there to this very day ("Hagling"). The Féras and the Palées are definitely late spawners and they have been encountered in a state of spawning maturity as late as January and even in February. Other late spawners are the corregonines of Alpnach Lake and Lungern Lake, as well as certain tribes of the Gangfisch inhabiting the eastern part of Lake Constance. The "Winteralbeli" of Lake Lucerne and Lake Zurich also spawn late. Concerning the first of these, I know of isolated instances when I encountered mature specimens in the month of March. One fisherman maintained that "spawning Albeli" could be caught even later than that in the year.

The fact that the water temperature conditions affected the diet of the spawning maturity period cannot

be doubted. KOPPMULLER and SCHEFFELT have found that in the case of the blue corregonines of Lake Constance the critical temperature is 7°C. When this temperature is reached, the spawning begins. We have indications from other central Swiss lakes that this also applies to other types, perhaps the late start of sexual maturity of the Féras of Lake Geneva may be the result of climatic factors. Perhaps the lake's cooling down to 7°C (at that latitude) takes place later than it does in Lake Constance. On the other hand, it is amazing that the large corregonines planted in the Tessin already spawn in autumn in spite of the warm climate prevailing there. The summer spawners among the corregonines are those who spawn in the depths. They probably descend in August and September or perhaps even earlier into the cold spawning regions below where they encounter agreeable temperatures, but the problem is by no means solved by the determination of a critical spawning temperature, even though such a temperature may be universally valid. We must ~~presuppose~~ that the maturing of the gonads which takes several months must be "controlled" in some manner, a process in which the congregation into spawning swarms, the wanderings, and the change in nutrition as well as other factors play their rôle. It is certain that the reaction standards of the individual tribes are unequal, thus resulting in the very varied pattern of spawning habits of our corregonines which is shown in the following table:

TABLE SHOWING THE START AND THE DURATION OF SPAWNING PERIODS

(according to Fatio, revised)

Habitat	Species	Spawning Period
Lake Constance	"Sandfelchen" (Sand corregonine)	Middle of November to beginning of December
	"Weissfelchen" ("White corregonine)	End of November to middle of December (?)
	"Blaufelchen" ("Blue corregonine)	Beginning of December to middle of December
	"Kilch" (Beginning of June!)	End of October to middle of November

	"Gangfisch" ("Wandering fish")	Middle of November to December 25
Lake of Zurich	"Bratfisch" (Bodenblaalig)	End of November to middle of December
	Blaalig (Schwebblaalig)	Middle of November to middle of December
	Albeli	Middle of December to end of December
	Hagling	? Summer
Walen Lake	Blaalig	Middle of November to end of December
	Albeli (Sommeralbeli)	Beginning of July to end of October
Pfaffikon Lake	Albeli	Middle of November to end of November
Greifen Lake	Albeli	20 November to middle of December
Lake Lucerne	Balchen	25 November to 10 December
	Edelfisch (Noble fish)	1 August to 20 August
	Albeli	1 July to 15 September
	Winteralbeli	December to February
Zuger Lake	Balchen	20 November to 15 December
	Albock	15 September to 31 October
	Albeli	?
Lake Brienz	Balchen	End of November to 15 December
	Albock	5 September to 25 September
	Brienzlig	10 October to 20 October
Lake Thun	Thunerseebalchen	5 December to 15 December
	Albock	5 September to 25 September
	Kropflein (Brienzlig)	20 August to 10 September
	Kropfer	1 September to 15 October
Sempach Lake	Ballen	15 November to beginning December
Baldegg Lake	Ballen	25 November to middle of December
Hallwil Lake	Ballen	15 November to 10 December
Lungern Lake	Felchen	30 January to 15 February (?)
Sarner Lake	Felchli	15 January to 15 February
Lake Ageri	Corregonine (Balchen)	20 December to 15 January
Lake Neuchatel	Palée de bord	1 November to 20 November
	Palée de fond	20 December to 15 February
	Bondelle	1 January to 20 January
Lake Bienne	Pfarrig	10 December to 1 January
Lake Geneva	Gravenche	10 December to 25 December
	Féra	1 February to 15 March

SPAWNING LOCATIONS, HOMING INSTINCT, AND LOYALTY TO CERTAIN AREAS OF THE INDIVIDUAL TRIBES

First of all we have to decide whether one and the same tribe of corregonines seek the same place year after year in order to deposit their spawning product there. A poll of fishermen which we conducted did not result in a uniform pattern of replies. Generally speaking it was reported that the shore corregonines select very definite locations right on the shoreline, and spawn there exclusively, so that there is no purpose in looking for them anywhere else. In addition to this there are such examples as the fishermen of Lake Lucerne who successfully concentrate their efforts year after year on the depths near the steep banks of the almost vertical walls of rock ~~where they encounter spawning Edelfisch~~ where they invariably encounter "Edelfisch" during the spawning period. The following rule applies for Sempach and Hallwil Lakes: the corregonines congregate at certain locations for the spawning period. These spots are well known and regularly yield good catches of corregonines during the spawning period. The situation is quite different in the case of tribes spawning out on the open lake or on the surface above deep water. Their spawning is governed by the conditions prevailing in that particular year, that is to say they sometimes spawn at greater sometimes at lesser depths. Occasionally they spread out over a considerable variety of depths during the spawning period and then they are difficult to catch. In this connection the following details should be noted:

While according to WAGLER the "Blaufelchen" (Blue corregonine) spawns directly below the surface above the deepest spots of the lake, the larger floating corregonine tribes of the other lakes seek out the shoreline, while others again, such as the "Edelfisch" (Noble Fish) of Lake Lucerne

and the "Balchen" of Zuger Lake descend to great depths of 100 metres and more. The "Albock" of Lakes Thun and Brienz, the "Féras" of Lake Geneva, as well as the "Palées de fond" of Lake Neuchâtel and the "Kilch" of Lake Constance are also "depth spawners".

Several tribes of Lake Zurich, Walen Lake, as well as the "Albeli" of Lake Lucerne, the "Brienzlig" of Lake Brienz and Lake Thun and the "Albeli" of Pfaffikon Lake and Greifen Lake which have, in the meantime, died out, as well as the "Ballen" of Lake Sempach all spawn at "half depths".

The following are "shoreline spawners": the sand corregonines of Lake Constance, the "Balchen" of Zuger Lake, Lake Lucerne, Lake Thun and Lake Brienz, the "Ballen" of Hallwil and Baldegg Lakes, several larger tribes of Lake Wallen, as well as the "Gravenches" of Lake Geneva and the "Palées de bord" of Lake Neuchâtel.

On several occasions it has been pointed out that in lakes which are subject to progressive eutrophication the corregonines which were in the habit of spawning in the depths are changing their habits and becoming shoreline spawners. In this connection one question must, however, be left unanswered, namely whether the tribes previously spawning in the depths have not died out as a result of the worsening of their living and development conditions, and whether new populations composed of new stock planted in most of the lakes have not formed themselves in their place. There is reason to suppose that this happened in the case of the corregonines of Sempach Lake, the population of which was strongly affected by the introduction of stock from other lakes over a period of years. It has been established that in Lake Geneva too, the spawning habits have changed considerably over a period of several decades after the introduction of corregonines from the lakes of the Savoy

region and in particular from Lake Neufchâtel. In view of this we generally base our observations on bodies of water in which the old stocks continue to dominate and in our compilation we attempt to take into consideration the reliable data available from the works of earlier researchers.

DESCRIPTION OF SPAWNING GROUNDS.

Corregonines divided by type of spawning ground

sand and gravel:

sand corregonine of Lake Constance
"Gangfisch" of Lake Constance
"Albeli" of Greifen Lake and Pfaffikon Lake
"Palée de bord" of Lake Neufchâtel
"Gravenche" of Lake Geneva.

on rocky stony shores:

"Balchen" of Lake Lucerne
"Balchen" of Zuger Lake
"Bodenblaalig" of Walen Lake
"Balchen" of Lake Thun.

more submerged plants, "hills" and "plateaus" far away from the shoreline:

"White corregonines" of Lower Lake
"Palée" of Lake Murten
"Palée de fond" of Lake Neufchapel
"Féra" of Lake Geneva (exceptionally)

on sandy and muddy ground in the depths:

"Kilch" of Lake Constance
"Bodenblaalig" of Lake Zurich
"Edelfisch" (Noble fish) of Lake Lucerne
"Albock" (Floating "Balchen") of Zuger Lake
"Albock" of Lake Brienz and, in part, of Lake Thun
"Bondelle" of Lake Neufchâtel
"Féra" of Lake Geneva.

out in the open water, fairly close to the surface but above great depths:

the blue corregonines of Lake Constance and other "floating" tribes which in some years do not descend all the way to the bottom.

THE SEX OF THE SPAWNING CORREGONINES

Previous observers have attached great value to the determination of the numerical relationship of the sexes. Frequently spawning period catches resulted in a considerably greater number of milters than spawners. The "sex index" usually indicated the strong preponderance of the males, e.g.:

"Edelfisch" of Lake Lucerne	687:100	(SCHEFFELT)
	513:100	(SURBECK)
Lake Thun	405:100	(SCHEFFELT)

Nevertheless, occasionally figures for one and the same tribe were very much lower in some years:

"Blue corregonines" 1911	529:100	
1923	161:100	

Outside the spawning period when floating nets and lines are used, these proportions are as a rule reversed. We have become convinced that it is impossible to obtain figures which faithfully reflect the actual state of affairs on the basis of net catches. During summer the nets tend to catch more spawners whose girth is increased by the maturing of the ovaries. The reverse applies to catches made with spawning nets. These are more dangerous for the males because there are many important signs indicating that during the spawning act the males among the bottom spawners keep closer to the bottom of the lake than the females. We paid particular attention to these relationships in the case of Lake Thun and Sarner Lake, and were able to establish that the females were usually caught at the top of bottom nets while most of the milters tend to get caught in the lower

part of the mesh.

The conditions are quite different in the case of of the blue corregonines which spawn out in the open water regions. In their case BAYERSDORFER and SCHEFFELT both have validly established that the males develop their sexual products more rapidly than the females and that they rise to the surface after reaching maturity and that they tend to remain there for an extended period of time while the females rid themselves of their load of eggs all at once, or at short intervals, after which they immediately descend to the depths once more thus avoiding the region of the floating nets. This is said to be the reason why the proportions of males to females found in spawning "floating corregonines" are invariably heavily weighted in favour of the milters. It is, by the way, commonly known that at the start of the spawning period the males caught outnumber the females while exactly the reverse is the case at the end of the spawning period.

Having examined all factors we arrive at a result similar to that achieved by WAGLER (Manual, etc.) namely that on the average the proportion of the sexes is fairly close to 1:1.

HATCHING

The Duration of the Hatching Period of Corregonine Eggs

The numerical values for the so-called "day degrees" (Tg) should be treated with great care. The Commission for the Investigation of Economic Questions of Fisheries which was established by the Swiss Fisheries Association and whose task it was to conduct the most thorough study possible of the breeding of corregonines was able to establish that while the hatching period for various corregonine species is considerably longer at low temperatures than it would be at higher ones, the calculated values in terms of so-called

"day degrees" are nevertheless significantly different for cold and warm bodies of water. This can well be illustrated by the following figures compiled by E. AMMANN:

Corregonine tribe	Temperatures	Duration of hatching period (days)	"Day degrees"
"Sand corregonines"			
"Albeli"			
"Floating Corregonines"			

(page 179 original)

It has also been established that the total of "day degrees" of corregonines hatched in relatively warmer water tends to be higher than that of those which develop in colder water. This means that while the lowering of the water temperature does slow down the development the duration of the hatching period is nevertheless not proportionate to the cooling-off of the water. In colder waters the eggs are hatched earlier than could be expected in accordance with the "day degree rule".

The temperature of the water is, incidentally, only one of the determining factors. The <u>amount of exposure to light</u> also influences the duration of the hatching period and probably the date on which the eggs are hatched is also influenced by the chemical composition of the breeding water. Light tends to stimulate the larvae in the egg to hatch more rapidly. A greater calcium content appears to have a delaying effect -- at least as far as one can draw any conclusions from several chance observations. Probably the degree of toughness of the egg-shell also plays a certain role for it is by no means uniform with the various tribes.

Finally it should be investigated whether <u>temperature fluctuations</u> of the water which ~~xxxxx~~ take place in the course of the development of the egg are capable of influencing the corregonines within. According to HOFER there is a tendency for sudden temperature drops to cause the increase in mortality which would mean that temperature drops during the hatching

period of "shoreline spawners" could also do harm out in the open water. On the other hand, other experiments (FUHRMANN, BIRRER and others) show that the newly hatched fry appears to be quite insensitive when it is transferred directly into colder or warmer water. We will deal with the question of the mobility of the fry, its dependence upon the water temperature, and its ecological significance in a subsequent chapter.

The hatching period, i.e. the time lapse from the hatching of the first to the hatching of the last fry of the same spawning also appears to depend, to a great degree, upon the spawning temperature. As far as could be determined in the course of experiments conducted in hatcheries, a lowering of the hatching temperature tends to increase the length of the hatching period. This was convincingly proven by E. AMMANN in the case of the coregonines of Lake Zurich. Rapidly incubated eggs thus result in fry which hatches within a relatively short interval. In one practical case the hatching period at 8°C was eight days, and at 3.8°C, twelve days.

THE STATE OF DEVELOPMENT AND THE APPEARANCE OF THE COREGONINE LARVA AT THE MOMENT OF HATCHING

Coregonine fry from slowly hatched eggs tend to be more completely developed than those from rapidly hatched eggs. For this reason "cold water fry" and "warm water fry" of one and the same tribe may show considerable differences.

At one time it was thought that the size, shape and pigmentation of freshly hatched coregonine fry differs from tribe to tribe and could even be used for the characterization of the species. This is stated in many detailed illustrated reports by NUSSLIN, SCHEFFELT,

WAGLER, THIENEMANN and STEINER. Specifically, these authors believed that in the blue coregonine of Lake Constance they had found a type whose larva could be identified by its short body-length, large round yolk-sac, and weak pigmentation, while the "sand coregonine" was longer, had a small oval yolk-sac, and was equipped with larger and more numerous pigmentation cells. These authors believed to have noted that there are two basic groups of coregonines which can be differentiated by their structure in the larval stage and that the diminutive size of the larva was connected with the denser gill raker filters of the adult fish, and the larger size of the larva with the looser gill rake filters of the fish feeding on larger animals. But SCHEFFELT already pointed out that individual varieties, such as the "Gangfisch" ("Wandering fish") of Lake Constance do not follow this rule.

We devoted particular attention to these problems because we were especially interested to establish differential diagnosis for groups which could be systematically differentiated. We compared the freshly hatched-out larvae of various tribes -- e.g. the small Albeli of Lake Lucerne with those of the Féras of Lake Geneva -- and we were also able to incubate one part of the same spawning at a lower and another part at a higher temperature in order to test and study the effect of a shorter or longer period of development upon the appearance of the fry. From the material thus gained we are publishing some examples, and in this connection we have been able to establish that the appearance of the fry (larvae) primarily reflects its degree of maturity. Premature births tend to be small and have a relatively large yolk-sac and little pigmentation, while, conversely, fry which have been hatched out late tend to be longer, smaller yolk-sac, and more numerous pigmentation cells. (See Figs. 19 and 20).

Illustration No. 19 on p.181 of German text -- Freshly hatched-out one-day-old coregonine larvae from Lake Bienne. The two on top underwent slow incubation at low water temperatures and hatched out late. They have a small oval yolk-sac. The lower two were rapidly incubated at higher water temperatures. They hatched out early and have large spherical yolk-sacs. "Premature birth". Since these larvae belong to the same race, and originate from one and the same spawning, these differences are the result of environmental factors and are of no genetical significance.

Illustration No. 20 on p.182 of German text -- Freshly hatched-out coregonines. Left: "Warm water fry" hatched out early, weak pigmentation. Right: "Cold water fry" hatched out late, strong pigmentation.

As a result of the experiments conducted by E. AMMANN at Stäfa, it has been established that eggs incubated in cold water already acquire a considerably darker colour, sometime before the hatching-out date, than eggs of the same origin which have been incubated more rapidly. We might also point out that SCHNAKENBECK (1934) thoroughly investigated the black chromatophores of coregonine fry of various tribes and that he denies the existence of a fundamental difference between the different types. We believe that exactly the same applies equally to measure for the yellow chromatophores. We are convinced that the differences reported by NUSSLIN and others are the result of differences in incubation conditions and of a varying degree of maturity. In stating this we, by no means, wish to claim that the individual tribes show no differences in size, shape, pigmentation, etc. of the larvae, but a final judgment will have to be reserved until eggs of varying origins can be hatched after incubation under exactly

identical conditions. It has been established that the first-born of the same spawning by no means show morphological agreement with those born afterwards. In this connection we have recorded certain observations concerning the "Gangfisch" of the Lower Lake of Lake Constance. The following figures are submitted in support of our statement:

Body length divided by maximum diameter of the yolk-sac: L/D

in the case of freshly hatched fry at the beginning of the hatching-out period: 6.6

in the case of one-year-Old fry at the end of the hatching-out period: 10.4

THE BEHAVIOUR OF THE FRY IMMEDIATELY AFTER HATCHING OUT

No sooner has the larva left the egg than it starts to swim vigorously and ~~constantly~~. In view of the fact that such freshly hatched out fry is for the time being incapable of taking nutrition, it is really hard to understand why they swim about so vigorously. Their mouth is still closed. They are still incapable of starting a hunt for other organisms. This restlessness of the fry which naturally consumes a great deal of energy and thus also a great deal of the nutrition contained in the yolk-sac can, in our opinion, be explained by another biological phenomenon which may be described by the term "dissociation". If the hundreds of thousands of freshly hatched out fry remain immobile at the spawning grounds a famine would soon ensue. It is thus vital that the young fry should spread over a greater space. When young coregonines are hatched in spacious aquaria or small ponds, then the originally very dense "hatching swarms" begin to separate and smaller wandering swarms form themselves through a peculiar form of "whirl dance" of the young larva. These smaller swarms then spread in various directions. This early dissociation movement is a biological necessity,

providing living space for the larvae who hatch out later, also makes sense for these movements to take place in colder water temperatures. This explains why the coregonine larvae swim so lively in even ice-cold water; ~~for~~ they thus stand the best possible chance of reaching zones with a more favourable temperature where their prospects for a successful feeding start are considerably better.

To date we have but little definite information concerning the orientation of the swarms. Light can be merely considered to act as a motion-provoking stimulus, but to date the existence of a positive ~~phototactic~~ phototactic active reaction could not be established with any degree of certainty. In unilaterally lighted containers the fry do not concentrate in the lightest areas but rather spread fairly evenly throughout the container. Their swimming energy appears to flag from time to time and the individual larvae start sinking gradually. After the elapse of a short period of time, the swimming motions become hastier ~~again~~ one more and the larvae again begin to ascend towards the surface.

At the expiration of a certain period -- estimated to amount to at least several days -- the individual animals begin taking notice of each other and occasionally follow one of their colleagues for a ~~little piece~~ short distance, only to separate once more. These are the origins of the so-called "whirl swarm" which has already been mentioned and which later becomes the wandering swarm when the older members of the hatching swarm join together, while the freshly hatched out larvae continue their disoriented swimming about. We must assume that some form of "permanent swarm" or "age-group swarm" which are so characteristic of the coregonines have their origins in these early days.

In the course of our hatching experiment we were soon able to observe almost continuous circuitous

movements on the part of young coregonine swarms. Hundreds of individuals took part in these movements. Whenever the swarm came into the region of a water current, they usually took ~~real~~ tactic counter~~action~~measures against it. Their progress against the stream (current) was evidently dependent upon their swimming energy. ~~On~~ In some places they were just capable of counteracting the current and they therefore devoted all their energy to maintaining their position without progressing forward. The direction of light rays in no way influenced them in doing this, but they did appear to be capable of using each other for orientation, that is to say that a fellow-member of the swarm swimming past an individual apparently triggered a stimulus to join and follow him. In containers in which there were no currents this fish-to-fish orientation evidently was the main stimulus for the cohesion of the swarm and the "advance guard" of the group appeared to be effective as guides or leaders. Occasionally stragglers could also be noticed. They were individuals who were not capable of following the swarm for an extended period of time, and they finally became separated from it.

From these observations in hatching containers and ponds, we can deduce certain assumptions concerning the behaviour of young coregonines in open bodies of water which are their habitat. We wish to compile these assumptions -- with certain reservations -- here:

Upon the dissolution of the hatching swarm into wandering swarms certain guide or leader individuals take over the leadership. They are followed by a greater or lesser number of other individuals. When the young coregonines have become capable of feeding and when the swarm has reached a zone in which nutrition is abundant, the advance guard start hunting plankton, crabs and other food, and "co-operative" pasturing is initiated.

FUHRMANN has supplied us with valuable points of

information concerning the first meals taken by the young coregonines. We have also a fair idea of the menu of these first meals.

A noteworthy difference in the extent of the fasting period after hatching out exists between hatches incubated in warm water and those subject to "cold water incubation". The former tend to fast longer, for, at the moment of hatching out of the egg, it is, as we have already emphasized, not as well developed and not as richly pigmented, and is encumbered by a heavier yolk-sac than is the more mature "cold water fry".

Thorough and extensive observations conducted in hatching aquaria have shown that every single particle of nutrition, every tiny crab, is aimed at and snapped up in a shot-like forward movement. On numerous occasions Copepoda egg-sacs were found to be the main source of nutrition. Considerable quantities of them were frequently found in the stomach and intestines of the coregonine fry. More recently QUARTIER, however, expressed doubt as to whether coregonines are capable of digesting these eggs. The author pointed out that the eggs, when they leave the intestines of the coregonines, are almost invariably still intact. It has, however, been established that frequently the carriers are swallowed together with the egg-sacs and it is most unlikely that the thin chitinous cover of a Cyclop or a Diaptomus can resist the digestive juices of the young fish. Occasionally smaller and softer organisms, such as rotifera and protozoa also seem to be eaten. Occasionally a greenish colouring of the intestines of coregonine fry would tend to indicate that sometimes the young fry consume algae -- probably single-celled green chlorophyceae -- generally speaking there appear to be no difficulties in starting nutrition in hatching aquaria whose water supply consists of unfiltered sea water. A sufficiently

high water temperature is, however, a prerequisite. Below 6°C almost no nutrition is consumed. Sufficient exposure to light also appears to be necessary. The tables and curves (Figs. 21, 24) give a graphic picture of the increase in length and weight of the coregonine fry. The tabulations are based upon a large-scale breeding experiment conducted by The Commission for the Research of Economic Questions of Fisheries. In addition to the author, E. ALBIAN, Dr. FLORIN, Dr. WOKER and Prof. BECHERT (Lausanne) participated in the compilation.

Figure 21 on p.185 of German text:

The hatching of Palée fry at Lutry. On each date indicated in the left-hand column, ten specimens were caught, preserved and tested for length, volume and weight. This tabulation gives an insight into the effect of light and temperature.

Legend: Brut temp. -- Incubation temperature
Beginn. -- Start
dunkel - dark
hell - light
T - temperature
Datum der Konservierung - date of preserving specimens
Nahrung im Darm - Nutrition found in intestine
Länge mm 10 Stück - Length in mm. 10 specimens
Volumen cmm 10 Stück - Volume in cubic mm. 10 specimens
Gewicht mgr. 10 stuck - Weight in mg. 10 specimens

Figure 22, page 185 of German text:

Breeding of Lake Zurich coregonine fry at Stäfa. 65.3% of the "warm water bred" individuals died before the 36th day of age. The low temperatures to which the early hatched out fry was exposed (maximum 4.2°C) did not advance its rate of growth, while the late hatched out "cold water bred" coregonines achieved almost twice the weight in the course of their growing period (maximum 7.5°C).

Legend: Rapperswil - average temperature

Incubation period - 54 days

Stäfa: spring water, average temperature 6.2°
incubation period 60 days

Stäfa: sea water, average temperature 9.8°
incubation period 89 days

Age in days Incubation temperature in °C

Nutrition in intestines Mean length in mm.

Mean length in cubic cm. Mean weight in mg.

- -

Fig. 23 on page 186 of German text.

Curve showing the rate of growth of coregonine fry.

(Period March 18 to May 2. Temperature 9.5°C)

Legend: Weight in mg. Volume in cubic cm. Length in mm.

Weight Volume Length

- -

Fig. 24 on page 187 of German text.

Curve showing rate of growth of coregonine fry.

(March 18 to May 2. Temperature 5.6°C)

Legend: Weight in mg. Volume in cubic mm. Length in mm.

Weight Volume Length

- -

These figures clearly show the influence of temperature upon the rate of growth of coregonines fry. The fry loses its larval character as early as the second and third month of its life. The fins begin to consolidate and the shape of the fish becomes more muscular at the flanks. A curve plotting the rate of growth during the first month of life illustrates this (Figs. 23 and 24) for two different water temperatures. It is significant to note that at first no difference between large and small coregonines can be established. During the subsequent period the young small coregonines also keep step with their colleagues from large coregonine frys, even though they come from smaller eggs and have thus a somewhat less favourable start. The dwarfing is a

phenomenon which only becomes apparent much later, and it, as we have in the meantime been able to establish, does not primarily depend on the amount of nutrition consumed, but upon other factors, particularly the development of the sex organs. In connection with the pigmentation, it should be pointed out that all juvenile coregonines of the various tribes which we have been able to hatch and breed up to now have spots on their surface as long as they are young, and that this spotted appearance tends to disappear with the completion of the first year of life (Fig. 25).

Figure 25 -- Alpnach Albeli; note spotted appearance of juvenile fish in summer.

This reminds us of the spots found on the grayling which, as is well known, persist throughout the life of this fish. We are also reminded of the spots found on young trout and salmon and of the juvenile appearance of other fish species whose spots and dots differentiate them from their elders. In exceptional cases we also encounter indications of this juvenile pigmentation in older, larger fish of certain tribes.

MONOGRAPH OF THE SWISS COREGONINES

A Contribution to the Problem on the Formation of New Species

By Paul Steinmann, Aarau

Received June 15, 1950

Special Part

THE COREGONINE TRIBES OF INDIVIDUAL LAKES

Twenty-five of the lakes of Switzerland can be considered to be coregonine lakes. Several of them (Lake Murten, Baldeg Lake, Pfaffiker Lake, Greifen Lake) have, during the last few years, become so eutrophic that coregonines have become a rarity in them. Within the foreseeable future these lakes will probably have

to be struck off our lists. Others again have only become coregonine lakes in recent times, because at the time of the main movement of coregonine populations to our country they were not yet connected by waterways and could only be populated after the introduction of artificial coregonine breeding. Such lakes are: Aegeri Lake, Klontal Lake, Langen Lake, Lake Lugano, and Lac de Joux. Some lakes lying in the upper alpine regions accepted imported coregonine stocks temporarily, but proved to be unsuitable and the populations did not take root. Coregonine populations could also not be established in Lake Sihl, a lake created by new dam installations.

Our list contains all lakes which, at one time or today, had proven coregonine populations (cf. also Fig. 1 on p.110 of German text).

LIST OF SWISS COREGONINE LAKES

Regio rhodanensis (Rhone region):

Lake Geneva (Lac Léman)
(The Savoyard coregonine lakes located on French territory will be dealt with only in an appendix)

Regio jurassica (the Jura region):
Lake Neuchatel, Lake Bienne, Lake Murten, Lac de Joux

Regio arurensis (Upper Aar):
Lake Thun, Lake Brienz

Regio intermedia (Central region):
Sempach Lake, Hallwil Lake, Baldegg Lake, Greifen Lake, Pfaffiker Lake

Regio riusensis (Reuss region):
Lake Lucerne, Sarner Lake, Lungern Lake, Lowerzer Lake, Lake Aegeri

Regio lindimacensis (Limmat region):
Lake Zurich, Walen Lake, Klontal Lake

Regio bodanensis (Lake Constance region):
Lake Constance, Lower Lake

Regio transalpina (previously free of coregonines)
Lago Maggiore, Lake of Lugano

The character of these bodies of water will be discussed in the introductory paragraphs concerning the individual lakes. Their original interconnection during the glacial or post-glacial period will be discussed in the systematical-genetical part with the aid of a special map chart.

A. LAKE THUN

Although the surface of Lake Thun, with its 48 sq. km., surpasses that of Lake Brienz by 18 sq. km., its volume is only greater by 1.4 cu. km. This is due to its lesser mean depth (135 meters); at its deepest point it is 217 meters.

INTRODUCTORY REMARKS

If we put this lake ahead all the others, we have very special reasons for doing so. I received far more coregonines from this lake than from any other lake. I was entrusted by the Cantonal Directorate of Forestry of the Canton of Berne to separate the "types" found in Lake Thun and describe them in order that practical conclusions for the fisheries management of the lake could be deduced. As a result, I got in touch with all professional fishermen and also many amateur sports fishermen of this body of water during the years 1937/38 and, in particular, during the period 1939-1945. I was thus able to obtain a great variety of coregonine material at varying times of the year from all parts of the lake. Indeed I even had the opportunity to organize special test catches with apparatus I considered suitable, and also with types of nets previously not used in this area. These investigations formed the basis for subsequently conducted further studies which gradually took in more extensive areas and finally encompassed all the coregonine lakes of Switzerland. Unfortunately, the plan to conduct a general revision of the classification of the coregonines of Switzerland only matured with the passage of time. For this reason the material from Lake Thun was not utilized and registered as thoroughly as may have been desirable. Thus, many of the fishes caught at the start of the investigation were merely measured, weighed, and the gill rakers examined while other data was not obtained, and

the sex and age was not always recorded. Further supplementary investigations were able to fill these gaps to a certain ~~degree~~ extent and today I feel that I can consider Lake Thun, together with Lake Constance, as the most thoroughly investigated coregonine lake.

METHODICAL

In line with my entrusted task, I allowed various fishermen to demonstrate and explain the "types" encountered in Lake Thun. Without prejudice I noted the names given to me, took measurements and weights, recorded them, and in most cases I also determined the age and the degree of maturity, as well as the number of raker thorns (teeth?) of the first gill arch, and I also took a great number of photographs. I started out in the hope of soon being able to learn to differentiate between the four different forms which WAGLER considers to be the "coregonine species" of Lake Thun, but this hope was to be disappointed. When one issues instructions to a fisherman or a fisheries supervisor to obtain a "Kropfer", an "Albock" or a "Balchen", then one can expect with some degree of certainty actually to obtain the desired type, but I also encountered fishermen who merely described the "large and small coregonine" by the currently fashionable names in the fish trade, namely "Féra" and "Bondelle" and who did not want to know anything of a differentiation of large coregonines into "Albocks" and "Balchen" and of small coregonines into "Kropfer" and Brienzlig". I then made the following experiment. I selected the most reliable of the fishermen and presented them with 20-30 coregonines of approximately the same size, requesting them to "sort" them. Without exception they proved to be very unsure of their judgment. Mostly they were able to label individual specimens with certainty while disagreeing on others. Several fishermen told me

with great conviction that it is only possible to differentiate fully mature fish during the spawning period. Throughout the rest of the year it was, so they said, seldom possible to state anything definite concerning the grouping to which an individual fish belongs. The "Kropfer" was said to be the least difficult to identify, but it too was said to form "bastards" with other types. This is not only the case on Lake Thun, but, as I was to find out later, in other locations as well. Invariably the fishermen excused themselves by blaming the "bastards". In this connection it must, however, be recorded that the "Kropfer" and the "Balchen" spawn at different times of year and that the remaining "types" also are distinguished at least by the fact that they spawn in different locations so that a hybridization or bastardization is hardly likely.

Under these circumstances I was, for the time being, left with only one alternative and that was to approach all the coregonine material delivered to me without prejudice and not to engage in any hasty premature labelling or classification, but rather to describe each coregonine as accurately as possible, to measure and to register it. To summarize the final result at this point: all four coregonine types of Lake Thun, differentiation of which no longer presents any particular difficulty to me, are connected with each other through intermediary types. The variability is completely continuous. Nevertheless, certain types do distinguish themselves and -- this I believe to be significant -- the "intermediary forms" between the individual types are, as a rule, found less frequently than the representatives of a distinct type.

In compiling the statistical data dealing with

the variations of the population, I kept closely to the method used by E. WAGLER. I also kept to the same criteria later on in the course of investigations of other coregonine populations, while, however, omitting some figures which to me appeared to be of no value.

First of all, I would like to give a review of the figures and indices I have statistically compiled (see Fig. 26):

1. Body length: (measured from the point of the head to the projection of the upper point of the tail fin onto the base line.)
2. Length of head: (measured from the point of the head to the rear edge of the operculum).
3. Circumference: (measured by drawing a string about the body immediately in front of the first dorsal fin ray).
4. Iris diameter: (horizontal distance measured by means of ~~dividers~~ calipers in the longitudinal direction of the head).
5. Adipose-caudal length: (measured with ~~dividers~~ calipers from the angle of the adipose fin to the beginning of the edge of the caudal fin).
6. Body weight:
7. Number of scales in lateral line: (only scales perforated by pores were counted).
8. Number of gill rakers on first left gill arch.

In addition to this in individual cases:

9. Length of pectoral fin.
10. Concavity of the caudal fin: (maximum distance of the edge of the caudal fin from the line connecting the upper and lower extremities of the caudal fin -- Fig. 6, p.139 of German text).

The following indices were calculated:

(a) The "Coefficient of plumpness" = body length ÷ circumference
(b) The "relative length of the head" (Length of the head expressed as percentage of total body length)
(c) The "relative size of the eye" (the diameter of the eye expressed in promilles of the total body length).
(d) The "relative adipose-caudal length" (this length expressed as a percentage of the total body length).

We omitted reproducing the numerical data in each individual case and have merely limited ourselves to a graphic representation of the relations. The numerical data comprised by us will be filed at the Museum for Natural and Local History and anyone interested may consult the typewritten copies filed there.

Figure 26 - p.344 of German text --
Re the variability of body proportions: Two two-year-old "Albocks" from Lake Thun caught by means of yarns in August, 1938. One-third of natural size: 1. slimmer type with pointed snout; 2. plumper type with blunt snout. In the latter the adipose caudal distance is considerably longer than in the former -- these drawings were used to record our statistical measurements: 1. body length; 2. circumference; 3. length of head; 4. diameter of eye; 5. length of pectoral fin; 6. adipose-caudal length; S number of scales; K number of gill rakers on first gill arch.

AGE

If we survey all the material investigated by us, consisting of more than 1,000 fishes of the most varying size and origin from all possible zones and depths of the Lake, then we can state that the age of the fish we encountered varied from a few months to six years, none being older than that, and that the overwhelming majority was from two to five years old. Other lakes we know of considerably older coregonines. We still do not know with any degree of certainty why we were unable to obtain any

specimens older than six years from Lake Thun. It may be that the relatively intensive fishing activities cut down the number of old fish so radically, but it also may be that the coreginines of Lake Thun die a natural death at the age of five to six years. In this connection I am reminded of MILLER's observations concerning the small Marène which is also a "short-lived fish" and is, in many ways, similar to our "Brienzlig".

THE ABSOLUTE BODY LENGTH IN RELATION TO THE AGE

The length of the coregonines measured by us varied from 3.4 to 40 cm. The smallest sexually mature specimens were two years old and measured from 18 to 19 cm. Six-year-old ones were in part up to 40 cm. long but in part also considerably smaller. It is significant that frequently fishes of the same age are of varying length and fishes of equal size often have different ages. This "growing apart" already becomes evident during the first months of life. We now have to examine whether these considerable differences are the result of inherited characteristics (a varying growth potential) or are simply the result of environmental factors (quantitatively or qualitatively better or worse nutrition), or whether perhaps both these factors enter the picture.

In connection with this problem our investigation on very young specimens of coregonines are particularly interesting. On a single day in June, 1940, we were able to catch 43 such specimens in sizes from 3.4 to 17.3 cm. near Faulen lake (Fig. 14). None of them was older than nine months. In this connection it should be remembered that the spawning period of the coregonines of Lake Thun is spread over approximately five months so that the oldest could be nine months old while the youngest would be four months old. The differences in sizes which were determined

could thus, at least in part, be due to differences in age. On the other hand, the state of nutrition of these juvenile fish proved to be quite different. Without doubt the large summer-hatched fish had eaten more than the small ones, but the role played by the "growth capability" of the individual "tribes", i.e. the genotypical difference over and above that, could not be established with any degree of certainty. Nevertheless, it is significant that the plumpest specimens which showed the greatest similarity to "bottom albocks" (sand coregonines or "Balchen") which could be assumed to have the more rapid rate of growth were by no means particularly large. The definitely slim long-tailed specimens one could assume to be future "floating albocks" were of medium size. The longest among the 43 specimens were quite indifferent in their body proportions. In any case it was quite impossible to identify with any degree of certainty the "tribes" to which these 43 juvenile coregonines belonged. These small fish were by no means sufficiently differentiated to enable one to divide them into "floating" "bottom" "dwarf" or "deep lake albocks".

In this connection we would like to point to the most recent results of the investigations conducted by the Commission for the Research of Economic Questions of Fisheries. On instructions from the Commission, and at the special suggestion of Mr. Vouga, Messrs. ARMANN and BECHERT conducted a breeding experiment of young coregonines at different temperatures. In the course of this, a very strong dependence of the appetite upon the temperature was established. For this reason coregonines kept at low temperatures were severely retarded in their growth, while those raised in warmer water grew much more rapidly. In another part of our study we returned to this problem and here we would merely like to record that juvenile coregonines growing

up

up in the depths of the lake evidently remain smaller on the average than those inhabiting shallow waters.

Taking into consideration these aspects, the very considerable difference in the rate of growth (i.e. the "growing apart") of the young corregonines of Lake Thun observed by me, appears to have been caused in the main by environmental factors.

"THE COEFFICIENT OF SLIMNESS"

"Relative compactness" can be expressed either in terms of a relationship between the length and the weight, or the length and the circumference. Generally speaking, the circumference of compact fish will tend to be largest and that of slim fish smallest. But a single circumference measurement, for example that of the greatest circumference, is not the decisive factor. After all, the shape of corregonines can also be varied by the form of their tails. Thus, when the tail is relatively short and stout this can lead to the development of a compact type, the maximum circumference of which may be smaller than that of others. Relationship of length times weight in such cases gives more reliable comparative data.

Best proof of the great variability of compactness is obtained from the findings enumerated in greater detail below:

On November 3, 1939, a net was set at approximately 50 metres depth in Lake Thun near SCHERZLIGEN. Two corregonines brought up from this net had the following dimensions:

	Length:	Circumference:	Weight:
(a)	39 cm.	18.6 cm.	420 g.
(b)	36.5 cm.	21.6 cm.	500 g.

The "coefficient of slimness" in the case of

(a) 2.09
(b) 1.68

Both fish were male specimens. They both showed a strong spawning exzema and both exuded "milk".

Neither in the number of their scales nor in the arrangement of their gill-raker thorns was there anything out of the ordinary which may have caused us to classify these two fish as belonging to different tribes. They were evidently members of the same age group of one and the same spawning swarm. By any standards, both of them would simply have to be classified as "Thunerseealbocks", and the fellow-members of their swarms of whom a further dozen was investigated showed average proportions. We have calculated dozens of coefficients of slimness and have established over and over again that in the case of the corregonine swarms of Lake Thun there are very great differences in slimness or compactness and that individuals which, on the basis of general criteria, could perhaps be included in certain "tribes" vary so considerably in the slimness of their bodies that the "coefficient of slimness" must be considered to be entirely unsuitable as a tribe differentiation characteristic.

Our Illustration 27 shows the entire population investigated by us in its length-weight-relationship. The individual "tribes" insofar as they could be differentiated on the basis of other characteristics are identified by different signs. On the average the "Bodenalbocks" (bottom albocks) appear to be somewhat more compact than the "Schwebalbocks" (floating albocks). It is certain that juvenile corregonines are slimmer than old ones.

Our Illustration 15 contains only the juvenile corregonines discussed further above. It shows the course of the rate of growth curve particularly clearly.

ILLUSTRATION 27 - pp.348-9 German text:

Record according to length and weight of all Lake Thun corregonines investigated.

Legend: typische Bodenalbocke = typical bottom albocks

typische Schwebalbocke = typical floating albocks

reife Albocke = mature albocks

unreife, dreijahrige Albocke = immature three-year old Albocks

reife Kropfer = mature "Kropfers" (Adam's apple)

reife, meist dreijahrige Zwergalbocke = mature dwarf albocks, mostly three-year-old

Jungfelchen und zweijahrige, unreife Zwergalbocke = juvenile corregonines and two-year-old immature dwarf albocks

Gewicht in gr. = weight in grams

Lange in cm. = length in cm.

RELATIVE LENGTH OF HEAD

We have calculated the length of head of the individual specimens in terms of percent of their respective body lengths and subjected the "head length indices" thus obtained to a variastatistical investigation (Illustration 28). The results show a total variation range from 15.6 to 19.1 cm. with the majority of the investigated specimens falling between 16.6 and 18.2 cm. If the "summer fish", which are not considered in our graphic representation, are also investigated, even higher indices would result. If the material is investigated in respect of the relationship of absolute body length and the index values, then it becomes quite evident that the small specimens have relatively large heads and the large ones relatively small heads.

This is clearly evident from the survey table reproduced on p.351 of the German text.

ILLUSTRATION 28 - p.350 German text.

VARIOSTATISTICAL INVESTIGATIONS II

OF CORREGONINES OF LAKE THUN

Legend: Anzahl Individuen = No. of specimens

Kopflange in % der Dorperlange = length of head expressed as percentage of body length

(Kopflangenindex) = (Head length index)

p. 351.- Variostatistical investigations of the corregonines of Lake Thun

Relationship of body length to relative length of head

Body length

Length of head expressed as a percentage of body length

Body length

Length of head expressed as a percentage of body length

Body length

Length of head expressed as a percentage of body length

Body length

Length of head expressed as a percentage of body length

ILLUSTRATION 29 - p.352 German text

Length of heads of corregonines of Lake Thun differentiated by "tribes". The specimens selected for this representation were designated by fishermen as belonging to the respective "tribes", and, in addition to this, they were found typical according to the criteria of the gill-raker apparatus and the number of scales. All les typical specimens were eliminated

from this investigation.

Legend: "Kropfer" = bottom albocks

"Brienzlig" = dwarf albocks

"Balchen" = shore albocks

"Schwebalbocke = floating albocks

The following table summarizes the results:

Size groups in cm. of body length	Head length indices expressed as % of body length

For reasons which were beyond our control it was not possible to evaluate fully all the data without exception, but the figures reproduced here show quite clearly that the rate of growth of the heads of corregonines is not equal to the rate of growth of their rumps.

This may, in the first instance, lead to the assumption that the length of the head simply decreases with age, i.e. that older fish have relatively small heads and young ones, on the other hand, relatively large heads. We have examined our material in this respect and the result we arrived at shows that this rule is not universally valid. True, in the case of large types of corregonines who reach lengths exceeding 30 cm. as early as during their fourth and fifth year of life, the rate of growth of the head decreases with age in relation to the rate of growth of the rest of the body. On the other hand, small types of corregonines maintain their relatively large heads throughout their lives, i.e. even in their fourth and fifth year of life they have "juvenile" proportions.

From our representation it is clearly evident that the "dwarfed" bottom albocks ("Kropfers") and

the also naturally small dwarf albocks ("Brienzlig") have large heads, and the large types, such as floating albocks ("Albocks") and the shore albocks ("Balchen") have small heads.

In summarizing it can be stated that the relative length of head can only contribute in the differentiation of the individual tribes if it is accompanied by a most exact investigation into the age relationships. Generally speaking, young corregonines have large heads. Those having a slow rate of growth maintain their relatively high head length index while those having a rapid rate of growth become relatively small-headed with increasing age.

ILLUSTRATION 30 - p.353 German text.

Variostatistical investigations of the corregonines of Lake Thun

Legend: Frequenzzahlen des Augengrossenindex = Frequency data concerning the eye size index

Zahl der Exemplare = No. of specimens

Gesamtmaterial 377 Exemplare = Total material 377 specimens

Augengrossenindex = Eye size index

RELATIVE EYE SIZE

What has been said in the previous section concerning the relative head length applies to a practically equal measure to the eye size: generally speaking, small corregonines are characterized by large eyes, while large (and old !) corregonines are characterized by a lower eye size index. Our table contains the mean eye size indices -- the diameter of the iris expressed in terms of promill of the body length -- by size classes from 10 cm. to 39 cm. body length. The graph representation shown in Illustration 30 gives a picture of the extraordinary great variation

range of the unsorted total material.

"Kropfers" were shown to have large eyes than Brienzlig, sand corregonines and albocks of the same size. This becomes particularly evident in the case of old Kropfers (unfortunately we hardly know any old "Brienzligs"). Evidently the relatively large eyes are connected with living in greater depths. Just what we want to say by this statement will have to be explained in greater detail further on.

Table at bottom of p.354 - German text

Eye size index according to size classes

(62 corregonines)

Size classes (length in cm.)	In promills of body length

Table at top of p.355 - German text

Eye size index according to "tribes"

(204 corregonines)

"Tribes"	In promills of body length
Albocks	
Brienzlig	
Kropfers	

THE RELATIVE CAUDAL PEDUNCLE LENGTH

In north European and, in part, also in central European studies with corregonines, the height of the caudal peduncle is usually given as a measurement which is of some significance in the characterization of certain "tribes". In view of the fact that, according to our experiences, the degree of lateral flattening of the caudal peduncle varies within wide limits, the "thickness" of the tail can

be determined accurately only by giving both height and depth measurements, but the measurement of the depth is connected with so many purely technical difficulties particularly due to the fact that the depth decreases continuously in the direction of the fin. For these reasons it appeared more promising to us to introduce another measurement for the characterization of the tail, i.e. the length of the caudal peduncle, which, when expressed in relation to the body length, i.e. as a caudal peduncle index, helps considerably in characterizing the various types of Lake Thun corregonines.

Table on p.356 - German text

Caudal Peduncle Length Index According to "Tribes"

(133 corregonines)

"Tribes"	Caudal Peduncle Length Expressed as Promill of Body Length
Unsorted	
Albocks	
Brienzligs	
Kropfers	

It is evident that the Brienzlig has a relatively long tail and that relatively short-tailed specimens predominate among the Albocks -- there were many bottom albocks among the specimens sampled --

- -

According to our measurements a caudal peduncle varies from a minimum of 5% to a maximum of approximately 10% of the body length. This is not to deny that between these two extremes there is a very great variation range within which hundreds of intermediary forms can be classified. Unfortunately our measurements are not without gaps and they are thus unsuitable for a statistical evaluation. Such an evaluation also would not be desirable until we are

able to differentiate more reliably between bottom and floating albocks.

SCALE COUNT

(Number of perforated scales located along the lateral line)

The scale count gives an indication of the relative size of scales. Large-scaled fish have fewer lateral line scales than fine-scaled fish.

In this connection we first of all made a compilation of the data extracted from FATIO's "Faune des Vertébrés" Vol. 2 (1890).

Table on p.357 of German text

	Scale count
"Albock", Coregonus wartmanni alpinus	
"Balchen" Coregonus schinzii helveticus	
"Kropfer", Coregonus exiguus albellus	

Accordingly, the "Kropfer" has the largest and the "Balchen" the smallest scales.

From our own material we have extracted several figures to characterize the variation range:

Scale Counts According to "Tribes"

(270 Corregonines)

"Tribes"	
Unsorted	
Albocks	
Brienzligs	
Kropfers	

If we again select the typical large corregonines from the total material then their scale counts are actually somewhat higher than those of the naturally small Kropfers and Brienzligs, but here again the variation range is very great and the differences find expression, if at all, only in the mean values. There is no tangible boundary line. Characteristics tend to fluctuate.

GILL RAKER TEETH AND STOMACH CONTENTS

It is improbable that the number and length of the gill rakers is subject to modifications caused by environmental factors, particularly not to the extent that the type of nourishment and the size of the individual bits of nourishment influence the structure of the gill rakers. It is, however, certain that the corregonines also show a very pronounced variability as to their gill raker apparatus, and that in view of the great variety available, certain living habits which differ from tribe to tribe will affect the process of natural selection. In this respect, our investigations dealing with the gill rakers of the corregonines of Lake Thun are particularly instructive.

If we compile all of the extensive material then we are able to determine that the variation range is unusually great as is evident from our graphic representation (Illustration 32), we encountered corregonines which had as few as 13 and others which had as many as 45 gill raker teeth.

Illustration 32 - p.358 German text

Variostatistical investigations of the corregonines of Lake Thun

Gill raker teeth counts on the first right gill arch of all corregonines with the exception of "large corregonines"

Legend: Anzahl individuen = No. of specimens

Anzahl Reusenzahne = No. of gill rakers

All intermediate values lying between these two extremities were also encountered. Since we were able to obtain a very great number of small corregonines (Brienzlig" and "Kropfer") whose gill raker counts

were diametrically opposed to each other, our curve quite clearly shows two apexes. The intermediate values (20-30) are relatively poorly represented and among the sexually fully mature "small corregonines" the values 23-27 are entirely absent. This fact particularly emphasizes the presence of two "small corregonine tribes" ("Brienzlig" and "Kropfer"). The gap thus caused is filled by 20-24 cm. long corregonines which include juvenile "large corregonines". As a matter of fact, two to three year old "Balchen" were examined on March 1, 1940, and invariably had gill rakers with intermediate gill raker tooth counts (24-28). The values were somewhat higher -- but still lower than in the case of the Brienzlig -- in the case of the "Albocks" or floating corregonines. The large corregonines of Lake Thun were shown to be intermediate forms.

If the gill rakers of the corregonines of Lake Thun are microscopically examined for secondary minute teeth and the location of supporting cartilages, then a great degree of agreement can be established. True, the "thorns" of the Brienzlig are somewhat longer and more pointed than those of the Albocks and the Kropfers, but the latter very strongly deviate from those of the "Kilchen" of Lake Constance, in spite of the fact that, as is known, WAGLER and others classified them as belonging to one and the same "species". Further investigations dealing with this will be necessary, but there are already various indications to the effect that the great similarity of the fine structure of the corregonines of Lake Thun and probably also those of Lake Brienz is an expression of their close relationship and their membership in a single "nation". As far as the thickness of the gill

raker teeth is concerned, it can be stated that it primarily depends upon the epithelia located above the cartilage which is subject to considerable changes. In the case of the "Kropfers" frequently very fine teeth are encountered, while normally corregonines inhabiting the depths of the lake, being consumers of nutrition found on the lake bottom, should have "large" teeth.

The examinations of stomach contents of which a considerable number was conducted, showed that the majority of large corregonines fed on plankton during the summer. But we still frequently also found insect larvae and other nutrition originating from the bottom of the lake, particularly in the case of large corregonines caught close to the shoreline. We became convinced that the nutrition of the large corregonines was mixed, at least part of the time. Perhaps this applies more to the "Balchen-like" corregonines and less to the "floating albocks". It is, however, certain that the "Kropfers" in the main, feed on pisidia and bottom crustaceans, while the "Brienzlig" feeds almost exclusively on plankton.

LENGTH OF THE PECTORAL FINS

The fin size in relation to the rump or also in relation to the head may also be of certain interest, since it is evident that the rate of growth of the rump, as expressed in the measurement of the body length, is by no means identical with the rate of growth of the extremities. Young corregonines have relatively smaller fins than old ones. In addition to this it appears that the bottom corregonines tend to have more elongated fins, while pronounced floating corregonine types have smaller fins.

Unfortunately, these relationships were drawn to our attention only at a relatively late date. As a result, we do not have any extensive measuring data based on our material from Lake Thun.

Table at top of p.360 - German text

Length of Pectoral Fin According to Tribes

(132 coregonines)

Tribes	In percent of body length
Albocks	
Brienzligs	
Kropfers, juvenile	
Kropfers, old	

It is noteworthy that the younger specimens have small and the elder specimens large fins:

Age in Years	Absolute Length in cm.	Pectoral Fin Index %
Kropfers		
Kropfers		
Kropfers		
Kropfers		
Brienzligs		
Brienzligs		
Brienzligs		
Brienzligs		
Albocks		
Albocks		
Albocks		

It is thus evident that the length of the pectoral fin is clearly dependent upon the age and is therefore not well suited for purposes of classification.

THE CONCAVITY OF THE CAUDAL FIN

During the very first period of life, the rear edge of the caudal fin is convex. Then the upper and lower points start to grow rapidly. They reach the approximate maximum of their length in a one-year-old fish. At that stage the concavity of the fin is particularly marked. Then the rate of growth of the middle part of the fin gradually increases, and, in the case of old specimens, the edge gradually

becomes straightened out. The concavity must be measured with the fin spread out flat, and it is difficult because the corregonines are often delivered with torn caudal fins. Since this characteristic is almost wholly dependent upon the age, and since it can contribute but little to the differentiation of the tribes, we merely took random samples. Following are the results:

	Young	Old
Albocks (bottom and floating albocks)	2.1-3.4	
Brienzligs	1.7-2.7	2.4-3.0
Kropfers	1.4-2.1	2.6-2.8

RATE OF GROWTH CONDITIONS

The age investigations which we, unfortunately, did not undertake in all of the 1,000 specimens examined nevertheless indicate that the rate of growth of large corregonines is considerably greater than that of the dwarf tribes. The Brienzlig had the slowest rate of growth. In this connection, we would like to emphasize what we consider to be the most significant finding, namely that the rate of growth of the corregonines of Lake Thun -- and in particularly that of the dwarf corregonines -- was very irregular. This observation completely contradicts E. WAGLER'S who, on the basis of his scale investigations, assumes a great uniformity of rate of growth of his four "corregonine species". We would like to quote the relevant section from WAGLER'S study of 1937:

"The rate of growth is a most outstanding characteristic of the Alpine corregonines, perhaps the only one which allows for a differentiation of the species when specimens of a certain size are available. Each species has its specific rate of growth which varies only within narrow limits in all the lakes in which it is found, and the mean value of which may perhaps be equal in all lakes."

In contrast to this, we established in the course of extensive breeding experiments, but also in the course of age determinations, that members of one and the same age group of the same tribe frequently differed considerably in size and individual specimens of the same size sometimes showed age differences of a year and, occasionally, even of two years. The latter applies particularly to the Brienzlig, which appears to grow but little during the latter part of its life. True, the members of one and the same wandering swarm frequently grow at almost the same rate. But in the same lake, and at the same time, corregonines of the same age but having entirely different body proportions have also been caught. It should be pointed out that in all these investigations the "net selection"error should be taken into consideration. WAGLER also claims to have considered this error, which, at a certain location, may easily camouflage the actual state of affairs by producing a catch of relatively uniform size, while larger and smaller fish are simply not caught in the mesh of the net. For this reason we insisted that the material we received from Lake Thun should also come from draw nets. When such draw nets are pulled in rapidly, then corregonines of various sizes can be caught. My position in opposition to WAGLER is primarily based upon such investigations.

I would like to express my own investigation results in the following sentences:

1. During the second year of their life, most large corregonines approach the 20 cm. boundary. They may even reach 23.5 cm. Some individuals lag behind and reach but 18 cm.

2. Three-year-old Albocks are 26 to 29 cm. in length,

Balchen occasionally somewhat larger.

3. Among the four-year-old large corregonines we found individuals measuring from 28 to 35 cm., the mean value being 32 cm.

4. Mean value of the oldest (4 to 5-year-old) individuals was 38.3 cm.

5. The Brienzlig at my disposal consisted principally of two-three-year-old specimens. Older ones were very infrequent and it is hardly possible to construct a satisfactory rate of growth curve for this tribe. The two-year-old ones were 17 to 19 cm. long, and the three-year-old ones 18 to 21 cm. Occasional 23 to 25 cm. long specimens were three to four-year-olds, but four yearlings could also be determined on several small specimens measuring little more than 20 cm. Unfortunately, scale investigations of these inhabitants of the lake depths were connected with considerable difficulties. The best rate of growth table was obtained in the case of the Kropfers.

Table on p.362 of German Text

	Mean	According to WAGLER
2 years		
3 years		
4 years		
5 years		
6 years		

It is noteworthy that all tribes have a good rate of growth during the first year of their life. After this, the Kropfer and the Brienzlig lag behind somewhat. As far as we were able to observe, the dwarf corregonines are preparing for their first maturity during the second, and particularly the third, year of their life, while the large corregonines only mature in the fourth year. Thus their third year is the year of their greatest growth.

CHANGES IN SPAWNING HABITS IN THE COURSE OF DECADES

Another not insignificant factor should also be noted. During the 19th century the Albocks of Lake Thun spawned as early as September. For this reason, the closed season was set from September 15 to the end of October until 1908. After Albocks in their complete mating regalia were encountered as late as the end of November, it was decided to start the closed season a whole month later. Thus the closed season for the Albock came into the closest proximity of the main catching season for "Balchen". The latter, mostly large specimens, according to GILLIERON, a fisherman at Scherzligen, spawned on loose rocks close to the shoreline in location of various depth, breadth, and width. Changes in the spawning habits -- both as to time and place -- have been reported from various lakes. In this respect too the corregonine appears to be quite variable. Today the spawn catching period of the bottom Albocks practically coincides with that of the floating Albocks.

More recently, considerable numbers of large corregonines have been introduced into Lake Thun by means of artificial breeding, while Kropfers and Brienzligs are caught by means of depth nets during the very spawning period. In this connection, a few figures:

Year	No. of spawning fish	Weight in kg.	No. of eggs obtained
1912			
1921			
1922			
1924			
1925			
1926			
1927			
1928			
1929			
1930			

During the following years various changes in the fishing regulations take effect, and any comparison of figures would, therefore, only have limited validity. Assuming an average weight of 250 g. per fish, the total catches from 1932 onwards, according to statistics compiled by professional fishermen, show the following figures:

Table at bottom of p.363 - German text

1932	1935
1933	1936
1934	1937
1938	1944
1939	1945
1940	1946
1941	1947
1942	1948
1943	1949

There are still some gaps in our knowledge concerning the living and spawning habits of the Kropfer and Brienzlig, since these ecotypes almost continuously inhabit considerable depths. It appears that both of them are widely distributed throughout the year, evidently split up into small swarms which enable them to hunt for nutrition. During the height of summer they join together in larger associations, and during that period they can be caught at suitable depths -- occasionally quite deep -- in large numbers. Their spawning places are 50 to 100 metres and even more under the lake surface. They spread over considerable areas of the lake bottom. Nevertheless, fishermen do know individual preferred locations in which the fish can be caught with particular success. Throughout the remainder of the year outside of the spawning period, the Kropfer and the Brienzlig like to keep to the deeper parts of the lake, and only in shallow inlets do they approach the shallower zones closer to shore. Kropfer as a rule remain in the depths.

If they are exceptionally caught closer to the surface, then they do not bloat and they look more like Albocks than they do when they originate from the depths. The rapid spoilage of the "soft" meat and the poor keeping quality as well as the fading of the colour, are all connected with the difference in pressure to which they are subjected when they are suddenly pulled from the depths to the surface. The same also applies to the Brienzlig when it is caught at great depths.

CONCERNING THE MIGRATIONS OF THE CORREGONINES OF LAKE THUN

Contrary to the opinion previously current, the corregonines by no means keep to standing bodies of water. The Albocks of Lake Thun also undertake extensive migrations not only from inlet to inlet within the lake, but also into the Aare Canal, Interlaken, where they may be encountered in large numbers as early as in the summer months. Particularly during the last few years this migration phenomenon has become very pronounced. Unfortunately the streams connecting Lake Thun with Lake Brienz become impassable through the construction of industrial installations, so that swarms of corregonines often pile up for months at a time at the bottom of artificial waterfalls. In various respects this has had a most unfavourable effect. Recently epidemic diseases have broken out among these "corregonine jams" and they pose a serious threat. According to the nature of the corregonines, communications between the lakes should be kept open so that the fish freely seek their feeding or spawning locations according to their wishes and requirements. In connection with our genetical problem, the noticeable migratory urge of the corregonines of Lake Thun is interesting because it is an indication of remnants of

the anadromous urge of its forebearer the original corregonine.

SUMMARY OF THE RESULTS OBTAINED IN LAKE THUN AND COMPARISON WITH INVESTIGATIONS CONDUCTED IN OTHER LAKES

The variability of the Lake Thun corregonine is very manifold, but it is difficult to draw precise lines separating the individual tribes. We have to assume a central type of average build which we make the "Primigenius" and which, in the case of Lake Thun, could be called either "Bodenalbock" or "Wanderalbock" (bottom albock)("wandering albock"). This is, in fact, the type which has been called "Balchen" by many fishermen but which shows no evidence of any direct relationship with the "sand corregonines" of Lake Constance and of eastern Switzerland and which could rather be classified as being related with the "Weissfelchen" ("white corregonine") of the lower lake of Lake Constance and of Lake Constance proper. We call this type

Coregonus lavaretus L. nat. arurensis ecotype primigenius

The bottom corregnine in Lake Thun generally prefers the submarine hills but it also lives in the zone of free water and in its body proportions, and in particular, its gill raker teeth, it is very close to the large corregonines of French Switzerland, the Féra of Lake Geneva, the Palée of Lake Neuchatel, and the Pfarrig of Lake Bienne. The fact that it is today called "Balchen" is directly due to a fisherman from eastern Switzerland, who, it has been established, introduced this new name after he had moved to Lake Thun because certain morphological ecological characteristics of this fish reminded him of the "sand corregonines" of the eastern territories.

By way of contrast, let us compare the gill rakers:

	Gill Raker Teeth	
"Sand corregonines" of Lake Constance	"Balchen" of Zuger Lake	"Bottom albock"
18-27	21-38	20-37

To date we have not been able to convince ourselves that in Lake Thun there is a strongly specialized shore corregonine such as those found in the Lower Lake or in Lake Constance. Occasional specimens having prominent high backs and the mouth located more toward the mandible side could be designated as

Coregonus lavaretus L. nat arurensis, ecotype litoralis but they evidently are very close to the primigenius.

On the other hand, very slim types of large corregonines which could be designated as "floating Albocks" have been encountered in Lake Thun. If a specific name is necessary, then they can be called Coregonus lavaretus L. nat arurensis ecotype pelagicus.

The spawning period of the albocks lasts from the end of August into January, with the "balchen-like" littoral types mostly appearing at the spawning places only in December.

The floating Albocks in Lake Thun have developed a dwarf tribe which leads a pelagic life in the deeper zones of the water. It is characterized by large eyes, numerous long fine gill raker teeth, and usually has light-coloured fins. This "Brienzlig", as this small corregonine is called, is quite definitely an early maturing type. It spawns as early as the second year of life and from that time onwards grows very slowly. Its spawning period is earlier than that of the floating albock. Usually it is as early as August and September, and is quite prolonged in duration.

We can call it "Zwergalbock" ("dwarf albock") and give it the name

Coregonus lavaretus L. nat. arurensis

ecotype nanus

I consider the "Tiefenalbock" ("depth albock") which has developed itself as a consumer of lake bottom nourishments from the depths of the lake (pisidia, Asellus cavaticus, Niphargus puteanus, Fredericella sultana and Chironomidae) to be a direct descendant of the primigenius. It has large eyes and scales, and its mouth is located slightly towards the mandible side, as is often also the case with the primigenius. Its gill raker filter is widely spaced, but still more delicate than that of the "Kilche" of Lake Constance which, in other aspects, is quite similar to it. The latter's head also has a somewhat different shape. Kilch and Kropfer should not be considered to be direct relatives. Their similarities should be considered as so-called conversion phenomena. They are the result of similar living habits, not of direct relationship. We will bring further details in the section dealing with systematics. We designate the "depth albock" or "Kropfer" as

Coregonus lavaretus L. nat. arurensis ecotype profundus.

The interrelationships can then be expressed by the following schematic diagram:

(p.367 German text)

Legend: Urfelchen: original corregonine
Uferalbock: shore albock
Schwebalbock: floating albock
Zwergalbock: dwarf albock
Kropfer:

our pictures are intended to illustrate the various types.

VARIATION RANGE OF THE LAKE THUN CORREGONINES

In the following table we have omitted uncertain specimens which we were unable to classify, and we have limited ourselves to specimens which, taking into consideration the various characteristics, we were able to assign to one of the categories with some degree of certainty. There are, however, also included some small specimens, which may influence certain measurements of characteristic body parts which vary with age.

Table, bottom p.367 German text

	In percent of body length			
	Circumference	Length of head	Diameter of eye	Caudal Peduncle
Albock ("Balchen")				
Schwebalbock ("Floating Albock")				
Brienzlig				
Kropfer				

	Pectoral fin length	Scale count
Albock ("Balchen")		
Schwebalbock		
Brienzlig		
Kropfer		

In summarizing what has been said above, we would still like to emphasize the following individual characteristics:

1. Albocks. It is difficult to differentiate between the "Floating type" and the "Balchen". When alive, both are fairly dark in colour and have blackish, rather small fins. The mouth is occasionally ~~somewhat towards the mandible side~~ sub-terminal, but occasionally also in the terminal position. The eyes are never noticeably small. Both types are close to the primigenius.

2. The Brienzligs are slim and silvery. Their scales have poor adhesion. Their fins, particularly their pelvic

fins, are usually of pure white colour. The eye is small (much smaller than that of the "Gangfisch" of Lake Constance -(macrophthalmus), which certainly is in no way related to the "Brienzlig", since it also strongly differs from it in its living habits (spawning habits)).

3. The Kropfer almost invariably has sharply pointed fins with a very dark apex. The tail is occasionally disfigured (heterocercal). The basic colour immediately after death becomes lighter brownish (reasons: the difference in pressure and temperature kills the fish which is raised from the depths rapidly, and also causes the change in colour. Kropfers caught closer to the surface appear to be less delicate and maintain their colouring).

Illustrations p.368-369 German text.

Illustration 33 -- "Schwebalbocke" (Floating Albocks) from Lake Thun with straight backs and noticeably small caudal fins. Spawner 32 cm. in length.

Illustration 34 -- "Balchen" or "Uferalbock" (shore albock) from Lake Thun. Spawner. 37.5 cm. 595 g.

Illustration 35 -- "Kropfer" from Lake Thun. Spawner 27 cm. in length, 245 g. 5 year-old-old gill-raker teeth - 20.

Illustration 36 -- "Albock" from Lake Thun, 3 years old, before first maturity, 27 cm. in length.

Illustration 37 -- "Brienzlig" from Lake Thun. Milter 20 cm. in length.

B. LAKE BRIENZ

Lake Brienz is located 567 m. above sea level. It is deeper than all the other Swiss lakes on the north side of the Alps (261 m.) with the exception of Lake Geneva which is somewhat deeper, but its average depth is greater than that of all the others, including that of the lakes of the Tessin. Its surface area is

only 30 sq. km. and its volume amounts to 5.2 cu. km.

The coregonines of this lake are similar to those of Lake Thun to the extent that here again there is a larger type and a dwarf type living alongside each other. Even Fatio already knew the small "Brienzlig". He called it Coregonus exiguus albellus, but considered this fish as infrequent. In contrast the "Albock of Lake Brienz" was classified together with the Lake Thun albocks and designated with the name Coregonus wartmanni alpinus. The name "Balche" current at that time is rejected as incorrect. According to Fatio, the albock of Lake Brienz remains somewhat smaller than the albock of Lake Thun.

Generally speaking, the coregonine fauna of Lake Brienz appear to be quite sparse around the turn of the century. No large coregonines whatever were caught, and even small ones only found their way into the nets occasionally. It was assumed that the temperature condition of the lake and the mud caused by the thaw waters of the Aare River impeded the development of the coregonines.

THE BRIENZLIG

During the First World War G. SURBECK (Footnote 1: Schweiz. Fischereiztg. - Swiss Fishing Journal - 25, 182 ff. 1917) attempted to establish more precisely the living habits, the density and the fishing possibilities as well as the breeding conditions for the "Brienzlig". Surprisingly, he was able to establish that the Brienzlig was by no means a rare, but a very common little fish, and that with suitable nets it could be caught in the thousands. Surbeck, at the same time, established that the Brienzlig was very fertile and that it became sexually mature and fit to spawn when it had reached a size of only 14-16 cm. Since then his observations have been confirmed many times. Because of the Brienzlig, special regulations had to be

issued, ~~because~~ as this fish never reaches the minimum measurements provided for in the Federal Fishing Laws.

I have investigated numerous Brienzligs caught during the last few years, and I have measured them. The rate of growth varies somewhat from year to year, but it always remains below the average of the other lakes. Even the delicate "Albeli" of Walen Lake and the "Weissfischli" ("Little White Fish") of Lake Lucerne are, on an average, considerably larger than the two Brienzligs of Lake Brienz.

WAGLER has paid particular attention to the coregonines of Lake Brienz and especially devoted himself to the Brienzlig. The results of his vario- statistical investigations are based on 50 specimens. My own measurements are in agreement with those obtained by Wagler.

I would like to give a few further absolute measurements.

Table p.371 German text

		Length in cm.	Weight in g.
1937:	Minimum		
	Maximum		
	Mean		
1938:	minimum		
	Maximum		
	Mean		
1944:	Minimum		
	Maximum		
	Mean		
1950:	Minimum		
	Maximum		
	Mean		

*A particularly slim specimen having a circumference of approximately 5 cm.

The Brienzlig measured were quite slim and only in exceptional cases did their circumference reach 50% of their body length. In the case of one 14.1 cm.-long two-year-old Brienzlig, the slimness record of 36.1% was established. The heads were large, most frequently 20% of the body length and more, and the eye diameter almost invariably exceeded 5% of the body length. On one occasion a maximum of 6.5% was noted, while WAGLER'S highest value was 6.2%, the mean being 5.7%. Here again the general rule, the smaller and younger the fish the larger the eyes, was found to be valid. The pectoral fins are long, occasionally very long. Here again we recorded a maximum of 17% which was considerably above that reported by WAGLER. All in all, the typical characteristics of dwarfing are more clearly evident in the case of older fish than they are in the case of younger fish.

The scale count of the dwarf form is not very low:

Minimum 71
Maximum 92
Mean 81.4

The gill raker teeth are long, fine and numerous:

Minimum 33
Maximum 45
Mean 40.6

My own lists contain 123 specimens. To this there should be added several winter spawners. I had, however, had previous opportunities to check Brienzlig catches and made short general notes on these occasions. In addition to that, I have at my disposal some notes concerning age determination. I therefore find it significant and important that a considerable number of Brienzligs reach maturity during the second year of their lives, and isolated ones even during the first year of their lives.

THE ALBOCK

Right up to the publication date of my

monograph, the "Brienzer Albocks" caused me considerable worry. FATIO was of the opinion that the Albock of Lake Brienz corresponds to Lake Thun, but that the former had a slower rate of growth, which was ~~caused by the environment.~~ due to environmental factors FATIO'S material consisted of two specimens and therefore his judgment must be accepted with great care.

"Le Albock, propre aux lacs de Thoune et de Brienz, un peu plus grand ainsi que plus abondant dan le premier..."

FATIO, without doubt, does refer to the Albock for he emphasizes the dark colouring of the fins which is, invariably, ~~missing~~ lacking in the case of the Brienzlig.

WAGLER also did not achieve much more than FATIO. He too had but two specimens at his disposal and he does not inform us of their lengths, but according to his rate of growth table, specimens must have measured some 25 cm. The probable age was three years. Perhaps the material investigated is somewhat too sparse to entitle us to make an assumption that these coregonines "in no way fit in the framework of the species". The reportedly very poor rate of growth is ascribed to the supposed lack of plankton.

I, too, in the beginning, tended to believe in this "starvation theory" until I noted certain circumstances which caused me to re-examine the question. In 1944, 1947, and 1950, I received typical large coregonines from Lake Brienz. Their proportions were, in ever way, up to those of the Albocks of Lake Thun. The three-year-old ones measured 30 and 32 cm., the four- and five-year-old ones 35 and 39 cm. One specimen weighed 650 g. The fishermen were unanimous in their reports about spawning coregonines which may reach weights of up to 1 to 2 kg.

I also received two-year-old Albocks which were definitely adipose and measured 22 to 25 cm. in length. Various random samplings of the stomach contents showed that the coregonines of Lake Brienz very evidently were

not suffering starvation. It may well be that during the height of summer, when the water is muddiest as a result of glacial flows, they feed less intensively than the fish of Lake Thun, but there is no sign of a starvation regime. To me, the large corregonine of Lake Brienz also seems hardly to differ from the Albock of Lake Thun. We also know that until most recent times "Wandering Albocks" ascended by way of that part of the river Aare, which connects the two lakes near Interlaken, and that they continue to start off on this migration every year and that only the dam built by man prevents them from completing it. I therefore see no reason at this point to consider this fish in any way different than the 'Albock'. As a wandering fish with a medium sized gill raker filter he belongs to the group of the Primigenius.

In this connection we would also like to compile a table which illustrates the variation range of the two ecotypes.

Table on p.373 German text

	Head length	Eye diameter	Caudal Peduncle
Albock			
Brienzlig			

	Length of pectoral fin	Scale Count	Gill Raker Teeth
Albock			
Brienzlig			

Legend: Mittel = Mean

Most recently Lake Brienz has acquired a special aspect through the appearance (or the rediscovery?) of a further very interesting "corregonine race", which, until further notice, we will designate "Winterbrienzlig", without, however, wanting to separate it from the Albock. In the floating nets of the "Brienzlig" fishermen, who catch the small dwarf-corregonines in the ten thousands, there

occasionally appear individual heavier pieces. With somewhat wider gauge nets they can be caught in greater numbers. They live together in swarms, as has been established on repeated occasions when they were caught with draw yarns. The main credit for first drawing attention to this 'race' goes to Mr. H. OSWALD, Fisheries Inspector at Interlaken, who did so in 1946. These fish achieve maturity in winter, when they have a length of 22 to 25 cm. and frequent the same spawning locations as the Albocks. The fishes submitted to me for investigation have a strong spawning epidermis, and were three to four years old. In appearance and colour, they were similar to the large Albocks. The sooty colouring of their fins is particularly distinct.

I now was particularly interested in the fact that several fish of the same size category, and even somewhat larger ones, were true adolescents, i.e. they had entirely undeveloped gonads, even though their scale pattern would have normally identified them as three-year-olds. These fish certainly belong to the true Albocks and they must reach a size of approximately 30 cm. before reaching maturity. By this factor only, but hardly by their appearance and colouring, did they differ from the "Winterbrienzlig."

And now arises the question, whether the 'Winterbrienzlig' represents an early maturing form, an ecotype nanus, or whether it simply is a "Early first Spawner" which will continue to grow later. Until we have further evidence we must accept the facts as they present themselves, and assume that partial populations separate from the population of large Albocks, mature at an earlier date and remain smaller in size than the majority.

I suspect that these 'Winterbrienzlig' are in

the process of doing what has ~~been~~ done before this the true Summer Brienzlig. The latter, which today spawn at considerable depths in late summer, have become ecologically isolated from the other race to such a degree that they can no longer be mixed with it. The "new" Winter Brienzlig has, as yet, not advanced as far in this direction. It still puts in an appearance at the Albock spawning locations, and, like the form from which it originates, it still spawns in winter. Perhaps it represents a race "in statu nascendi". I feel that for the time being it should not be considered a separate ecotype. The phenomenon is, as yet, too new. We therefore maintain our assumption that in Lake Brienz the Albock today appears alongside a dominant ecotype nanus, a very early maturing and highly dwarfed "Brienzlig". A tendency towards dwarfing also manifests itself in the case of the Albock, and it will be worthy of the attention of future researchers, but for the time being it cannot as yet be studied systematically.

Illustrations p.374-375 German text

Illustration 38 -- Albock from Lake Brienz.

Illustration 39 -- "Winterbrienzlig" from Lake Brienz. Milter 40 cm. in length, mature.

Illustration 40 -- True Brienzligs from Lake Brienz in August, immediately preceding spawning maturity. Top: male, mature, 15 cm. in length. Centre: female, mature, 16 cm. in length. Bottom: female, mature, 40 cm. in length. Body has been opened to show ovaries.

NOMENCLATURE

To summarize, we have established that the

two coregonine forms of Lake Brienz show such a measure of agreement with those of Lake Thun, and we have, therefore, no systematic reason for separating them. Consequently the correct name for the Brienzlig of Lake Brienz is

Coregonus lavaretus L. nat arurensis, ecotype nanus

and of the Albock of Lake Brienz

Coregonus lavaretus L. nat. arurensis, ecotype primigenius.

C. LAKE GENEVA

Lake Geneva is located 375 m. above sea level. Its average depth is 145 m. and its maximum depth 310 m. Its surface area is 582 km. Its volume 89.9 cu. km.

In the opinion of previous authors, two coregonine species are found in Lake Geneva. They are said to have come there from the region of the Rhine, probably in the direction towards Lake Neuchâtel by way of glacial or post-glacial waterways from the north or northwest. Under no circumstances can it be assumed that the coregonines of Lake Geneva have come from the Mediterranean area upstream to the Valley of the Rhône, for in general the fish fauna of the Upper Rhône and Lake Geneva clearly have the character of the fishes of north Switzerland, while the Rhone fishes below the "Perte du Rhône" are clearly of Mediterranean origin.

The question of the coregonines of Lake Geneva is, however, by no means solved by simply following JURINE and FATIO who assume the existence of two independent "good species" (Féra and Gravenche). The species descriptions available to us already give rise to serious doubts that these two types can be called species within the present-day meaning of that word. The question appears even more difficult when one inquires from old experienced fishermen or fisheries supervisors concerning the possibility of

differentiating between the two coregonines of Lake Geneva, and I became particularly critical after I subjected the majority of type examples displayed by Swiss museums to a comparative investigation.

It appears, that at the beginning of the 20th century, the so-called "Gravenche" has clearly become increasingly rare. In any case, coregonines spawning near the shoreline in December are only rarely encountered during the 20th century. In contrast to this, larger sized coregonines, preferring sloping submarine spawning grounds, have been caught in increasing numbers and used for artificial breeding. On the other hand, the spawning period of the "Féras" which, according to older authors, coincided with spring (February-March) now seems to have changed to winter. The object of the mass catches which the fishermen of Lake Geneva have been able to enjoy during the last few decades, therefore, is neither the Féras nor the Gravenche, in the original meaning of the words, at least not if we take the criterion of differentiating them by their spawning habits (location and time of spawning).

In the course of almost twenty years we have repeatedly had occasion to investigate and measure large coregonines from Lake Geneva. I find that their morphology has not changed significantly. The present-day "Féras" is not too different from that found at the time of FATIO. The variation range, however, appears to be larger. Ecologically speaking, fishes have changed considerably. Their spawning habits more closely correspond to those of the old "Gravenche". They are quite close to the "Palée" of Lake Neuchatel. The fact that the blood of the latter could become mixed with and may influence the surviving remnants of the former population,

as well as the fact that the alien fish introduced to the lake were able to maintain themselves, is not surprising, if one considers how small the catches were shortly after the turn of the century, and how massive the introduction of new stock from Lake Neuchatel, Lake Constance, and Zuger Lake, in order to prevent the "Féras" from "dying out". We bring some details concerning this in the section dealing with the "Management of Lake Geneva" (p.384 German text). On this occasion we would only like to emphasize that French efforts (p.384 German text) to acclimatize the "Lavaret" from Lac de Bourget have, to judge by our experiences so far, been unsuccessful. DOTTRENS will publish details in the near future. In spite of diligent efforts, I, too, have so far been unable to obtain small-sized floating or depth-coregonines from Lake Geneva. Since the depths of the lake have practically never been fished, we may, perhaps, still count on some surprises. According to my somewhat sparse figures, certain differences between the "Féras" and the "Palée" persist to this very day, and I will return to them in the chapter dealing with Lake Neuchatel.

In view of the fact that the present-day fish of Lake Geneva can no longer be identified with those of the last century, we must base our morphological observations primarily on the fairly numerous museum exhibits in our country and consult the descriptions compiled by ~~older~~ earlier authors. We have even taken the effort of going through the writings of V. FATIO in order to compile a confrontation list of differentiation characteristics which were supposed to separate the "Féras" from the "Gravenche" (old style). The following table shows the results:

	Féra	Gravenche
Gill raker teeth	not numerous (21-28)	fairly numerous (25-33)
Length of gill raker teeth	"relatively short"	"rather short"
Mouth	Towards the mandible side, occasionally subterminal	subterminal
Intermaxillary	"quite high"	"medium high"
Position of intermaxillary	slightly towards the rear, bent at the bottom	subvertical
Maxillary	usually reaching the edge of the eye	usually reaching the edge of the eye
Snout	rounded off,	almost rounded off
Caudal peduncle	fairly compact	short
Eye	small or medium	rather large
Pectoral fin	rather long	large
Pelvic fin	rather short	large
Vertebrae	60-63	59-61
Scale count	74-82	72-83
Mean body length	35-40	25-32

Let us at the same time also record the most important biologically ecological differences according to JURINE and LUNEL:

	Féra	Gravenche
Spawning place	depths	shore
Spawning period	February to mid-March	mid-December
Habitat(feeding grounds)	surface	depths
Growth (at maturity)	35-40 cm.	25-32 cm.
exceptionally	more than 50 cm.	infrequently towards 40 cm.

In my museum collection there are 9 Gravenche and several Féras from the period of V. FATIO, and, in part, even older. I must admit that without the aid of the label I could not possibly call the immature specimens Féra or Gravenche.

New measurements taken during the last few years show that juvenile Féras in some characteristics follow the description of the Gravenche and also agree with the old Gravenche ~~since~~ obtained from the museums for comparative investigation.

In the Lausanne Museum there is a 35 cm. long Gravenche from these bygone days, which shows a strong spawning ~~excess~~ ornament. Prof. ANDRE made available specimens measuring 24 and 25.2 cm. in length which had spawning ~~excess~~ ornament and which were proven to be four years old. On the other hand, I was also sent much larger specimens under the label "Gravenche" and I was in no way able to differentiate them from the Féras. One such specimen was a five-year-old female from Geneva, head length index, minimum 16.5, maximum 21.6, mean 18.6.

According to JURINE and earlier authors, the Gravenche differs from the Féra by its larger head (20.8% as against 17.7%). Our mean value is, however, considerably lower than that given by JURINE. ~~Particularly~~ Probably this is mainly due to the fact that the museums kept selected large specimens for their collections and these specimens have notoriously small heads.

If we now compare the measurements of five juvenile Féras, whose length varies from 21.5 to 22 cm., then we are able to establish the following trend in head length index:

Minimum	16.8
Maximum	17.7
Mean	17.3

For the large numbers of Féras from St. Sulpice which we investigated, we obtained the following:

Minimum	15.3
Maximum	16.6
Mean	15.8

and in the case of a series from Villette:

Minimum	15.3
Maximum	17.4
Mean	16.1

Thus the relationship between "Féras" and "Gravenches" again shows that the head length index of large corregonines is smaller than that of small corregonines, the Gravenche being a somewhat smaller type of corregonine in this respect, corresponds to juvenile immature Féra.

Large heads of characteristic of youth, and they also appear in the course of the dwarfing process.

The same applies to the eye diameter. In the case of the Gravenche, it varies from 3.7 to 4.4%, the mean being 4.1%. In the case of large Féra it is from 2.6 to 3.7% with a mean of 3%, and in the case of young Féra from 3.6 to 4.5%, with a mean of 3.9%. The length of the caudal peduncle expressed in percent is also noteworthy. In the case of the Gravenche it is Minimum 5.9%, Maximum 8.5%, Mean 7.6%. In the case of the Féra, Miminum 6.2%, Maximum 9.3%, Mean 8.4%, and in the case of juvenile Féra, Minimum 8.8%, Maximum 9.5%, Mean 9.1%.

According to these measurements, the Gravenches would appear to have relatively short tails but the differences are minor, and the variability is fluctuating.

In the matter of gill raker teeth, the Gravenche is in almost complete agreement with the Féra as to the number and length of the gill raker teeth. This is cearly apparent from our recent investigations. We are herewith reproducing our new figures in the form of a table:

Table top p.380 German text

Gill raker teeth

Gravenches

Féras

The corresponding figures for the Gravenches entirely fit in the distribution scheme of the Féras.

The scale counts also do not result in any useable differential characteristics:

Tables bottom p.380 German text

Scales on lateral line

Gravenches

Féras

In contrast the pectoral fin of the Gravenche is definitely longer than that of the Féra, and it appears that juvenile specimens of both types have shorter pectoral fins than older specimens. In this connection I would like to note specifically that my "Gravenches" were labelled as such by the respective museum directors and taxidermists and that I, for my part, can give no guarantee as to the correct designation of the fish. This particularly applies in the case of immature specimens.

Table top p.381 German text

Pectoral fin index

Gravenches

Féras

Gravenches

Féras

Gravenches

Féras

Legend: Mittel -- Mean

After all this it can no longer be seriously doubted that the Gravenche is merely a smaller form of the Féra, (i.e. one that does not grow as large).

Its peculiar characteristics, the large eyes and the long pectoral fins, are "dwarfing characteristics" which tend to become more prominent with age as is generally the case with the salmonidae.

There is no reason for assuming any genetical inter-relationship between the deep-water corregonines of, let us say, Lake Constance or Lake Thun, and the Gravenche. Even FATIO already energetically emphasized the differences between the "Kropfelchen" ("Kilchen") (i.e. the so-called "Adam's Apple Corregonines") and the Gravenche. He warns us not to consider these fish as identical.

In addition to the figures and coefficients of measurement given above, the following circumstances testify in support of the close relationship between the Féra and the Gravenche:

1. Previously these fish were not differentiated either by fishermen or by early scientists;
2. Even during FATIO'S times the Gravenches were sold on the market places of Lausanne and Geneva under the names of petits féras, féras blancs, féras jaunes;
3. FATIO himself emphasizes (l.c. p.248) that the Féras (evidently the older ones) as a result of their large fins strongly resemble the Gravenches, although large fins which are supposedly the most important characteristic of the Gravenches are not the sole criterion. Intermediate (transition) forms also seem to occur.

We must assume that what has happened in the other corregonine lakes has also taken place in Lake Geneva: the basic type in a given body of water has become differentiated into two main tribes. The Gravenche is a Féra which made the transition to life in the depths and it has become somewhat specialized there: large eyes, large fins, lighter colour, spawns more

towards the shore and somewhat earlier than the old Féras which only reached maturity in early spring. The Féras of the forties of the 20th century already advanced in spawning period (December-January), and it seems that they no longer spawn at such great depths as did the old Féra which, according to FATIO, reproduced itself at depths ranging from 100 to 200 metres, while our spawning Féras came from depths ranging from 20 to 70 metres. Whether originally transplantations of "Lavarets" or "Palées" contributed to this, or whether this change took place spontaneously, escapes our knowledge. It is, however, certain that the Féra itself is quite variable, while in the first instance it should be considered as a bottom corregonine, even though it certainly feeds on plankton part of the time, and possibly pelagical tribes have already been developed.

E. WAGLER (1939, p. 100) is entirely mistaken in his speculations. Basing himself purely on the previous abundance of this fish in Lake Geneva, he states that the Féra is "without doubt a floating renke". It therefore should be classified with the "Blaufelchen" (Blue corregonine) of Lake Constance, and should be designated Coregonus wartmanni. How one can choose to interpret falsely facts which are contrary to one's thesis can be seen from WAGLER'S following sentence:

"Only a small part of the Féra which has adopted different living habits, but which is not easily separated from the great mass, can still be counted as being a Féra according to the old nomenclature."

In other words, since the Féra does not fit into WAGLER'S scheme, WAGLER simply chooses to ignore the experience of the Swiss ichthyologists. He

ignores the relatively low number of gill raker teeth and the result of numerous stomach contents investigations, all of which clearly characterize the Féra as a bottom corregonine. FATIO, for example, writes:

"Sa nourriture semble consister principalement en mollusques, vers, insectes, larves de diverses sortes ainsi qu'en petits crustacés."

In our opinion the Féra of Lake Geneva is particularly close to the hypothetical original corregonine. Despite all its variability, it has still not split up into typical special tribes. The Gravenche should simply be designated as a small type Féra.

NOMENCLATURE

According to our nomenclature, we should use the following names:

Coregonus lavaretus L., nat rhodanensis, ecotype primigenius.

and

Coregonus lavaretus L., nat rhodanensis, ecotype nanus.

Table p.383 German text

Survey of Variation Ranges

	Circumference	Head Length	Eye Diameter	Caudal Peduncle
Gravenche				
Féra				

	Length of Pectoral Fin	Scale Count	Gill raker tooth count
Gravenche			
Féra			

In connection with the two corregonines of Lake Geneva, we have discussed two further corregonine names:

A "Bezola" - Coregonus bezola, FATIO 1890 - is said to be represented by the Gravenche of Lake du Bourget. Very little definite information concerning this fish is available. Evidently the Lac du Bourget contains in addition to the well-known "Lavaret" of the open water regions, with which we will deal below, also a bottom corregonine which was considered to be identical with the Gravenche. The name "Bezola" is therefore encountered in French Switzerland and fishermen also use it for the Gravenche of Lake Geneva and, presumably, also for juvenile Féra. I believe that this name has no real systematical significance.

A very old name for a corregonine of Lac du Bourget is "Lavaret". According to ROULE, and others, this name is intended to identify LINNE'S original type (Coregonus lavaretus LINNE 1758) upon which ARTEDI and RONDELET base their earliest descriptions. FATIO limits this designation to the floating corregonines of Lac du Bourget and those of Lac d'Aiguebette: small corregonines (15-30 cm. in length), shoreline spawners, spawning period mid-November to mid-December, gill raker tooth count 32-36, scale count 83-88.

We are of the opinion that the "Lavaret" is very close to the "Bondelle" of Lake Neuchatel, i.e. it is to be considered a floating form of the corregonine race. Here again it would, of course, be possible to consider convergence phenomena other than close direct relationships.

Addenda: While this monograph was in print, DOTTRENS

has published an extensive very interesting study on the Lavaret of Lac du Bourget. We will return to this study in a special publication. In this connection our museum also obtained several specimens of the Lavaret. Their investigations tend to confirm what we have written. According to my nomenclature the Lavaret should be called Coregonus lavaretus L., nat. rhodanensis, ecotype pelagicus.

ON THE HISTORY OF THE "MANAGEMENT" OF LAKE GENEVA

Until the turn of the century the net fishermen of Lake Geneva had strange concepts of conservation measures. As late as 1880, the minimum measurement for Féras was 15 cm. (!) and the nets usually had 3 cm. mesh. Reports concerning catches are contradictory and frequently entirely unreliable. In 1888 the large floating drift nets (Pics) were introduced and brought unexpectedly big catches but they soon gave rise to complaints concerning a rapid falling-off of coregonine ~~fishing~~ yields. F.A. Forel, the famous hydrobiologist at Morges, spoke of a "disparition partielle". Statistics were not kept at that time. Around 1904 there were still some 16,000 kg. caught in Lake Geneva. Later, even smaller catches were reported. According to PORCHET and COMBE, the yields then gradually began to increase in proportion to the increased introduction of new stock. We will return to these questions in the section dealing with economic matters, and here we would only like to record:

Table, bottom p.384 German text

Period	Catches of Féras and Gravenches	Amount of fry introduced annually

In the course of the stocking period which began in 1903, 250 million fry have to date been planted. Originally it was Gravenche fry and later, from 1923 onwards, fry brought from Lake Constance, Lake Neuchatel, and Zuger Lake. From 1929 onwards, the lake's own fry was used for artificial re-stocking. While this was going on, the French, as we have mentioned above, also introduced some Lavarets fry from Lac du Bourget. Altogether 1.1% of the fry of Zuger Lake and Lake Constance, 8.74% of the Palée fry from Lake Neuchatel and some 90% of Lake Geneva fry were planted in the lake. Today very many beautiful spawning fish are caught there, and the present stocking methods are entirely satisfactory. It should be particularly mentioned that some years ago "early summer fish" hatched from Féra eggs have been bred at the pumping station of the water supply installation at Lutry. By 1948 their number had risen to 81,400.

D. LAKE NEUCHATEL, LAKE BIENNE, and LAKE MURTEN

The largest of the lakes at the foot of the Jura, Lake Neuchatel, also had by far the greatest volume with its maximum depth of 154 m. and a mean depth of 64 m. With its volume of 14.2 cu. km. it ranges immediately after Lake Geneva and Lake Constance. Its height above sea level, 432 m., is the same as that of Lake Bienne. As the result of large dam installations near Nidau on Lake Bienne, the whole water system is interconnected for water storage purposes ("the Jura water control and correction scheme").

Lake Bienne is, in contrast to Lake Neuchatel, a shallower body of water. Nevertheless, it reaches a maximum depth of 75 m. and its mean depth is 28 m. Its area is 42 sq. km., and its volume 1.2 cu. km.

Lake Murten has become even more of a "pond lake" than Lake Bienne. Its volume is half that of Lake Bienne, in spite of its surface area of 27 sq. km. The maximum depth is 46 m., and the mean depth 22 m. Increasing eutrophication has caused this lake to change its character considerably during the last few decades.

The corregonines of the three lakes at the foot of the Jura show such a large degree of agreement with each other, that it appears advisable to view the system composed of these bodies of water as a whole. There are, in fact, connections between the three bodies of water which were not only used in the past, but continue to be used today. Thus the corregonines are given the possibility of wandering from lake to lake. According to FATIO, the large corregonines of this group of lakes shows a very pronounced wandering instinct and migrates annually upstream from one lake to the other, thus in autumn from Lake Neuchatel to the Broye into Lake Murten, or there are spawning migrations from Lake Bienne through the Zihl up into Lake Neuchatel. The smaller sized tribes, on the other hand, tend to live at greater depths and, as we will show further on, differentiation process between the three lakes has already begun to take place. For the group of lakes at the foot of the Jura, FATIO gives the following corregonines:

1. Coregonus schinzii, palea Cuv. et Val.

Lake Neuchatel; Palée, Palée de bord, Palée blannhe, Palée de fond, Palée noire.

Lake Bienne; Balaie, Balchen, Palchen

Lake Murten: Palée

Found in all three lakes.

2. Coregonus exiguus bondella Fat.

Lake Neuchatel: Bondelle or Bondèle

Lake Bienne: Pfarrit

Found in Lake Neuchatel and Lake Bienne.

3. Coregonus exiguus feritus Fat.

Lake Murten: Pferrit, Pferrig, Pfarrig, Kropfer, Férit

Found in Lake Murten.

4. Coregonus wartmanni confusus Fat.

Lake Neuchatel: Petite Palée, petite Féra, Gibbion

Lake Bienne: Balch-Pfarrit, Brater

Lake Murten: Pfarrig, Pfarrit, Ferit, Petite Féra

FATIO, in addition to this, differentiates between two forms:

a "stretched out" form which is more common, and a compact form having a higher back, the occurrence of which has become exceptional.

Illustration 42 - p.386 German text.

"Balchen-Pfarrig".

FATIO speaks of the Balch-Pfarrit of Lake Bienne with reserve ("forme voisine, peut-être composée").

To this there should be added various "bastards" or "hybrids" at least part of whom are said to be fertile.

Fishermen themselves continuously confuse these "forms". Some of them are not even prepared to recognize the independence of the "Bondelle" which they consider to be a juvenile "Palée".

In the face of this not inconsiderable confusion, we find that around the turn of the century two scientists from Neuchatel are devoting themselves to the clarification of the corregonine problem of the lakes at the foot of the Jura.

According to the findings of Prof. P. GODET, the Palée and Pfarrit have their habitat in all three lakes, the Bondelle, on the other hand, only in Lakes Neuchatel and Bienne. This author does not attempt a differentiation between the Pfarrit and the Férit (Footnote 1: P. Godet, Schweiz. Fischereiztg. 11, 74 1903).

Somewhat later (1904) Prof. FUHRMANN states his position in the same journal. His concept at that time can approximately be expressed in the following compilation: larger "floating corregonine type"analogous to the "Blaufelchen" (blue corregonine) of Lake Constance: Pfarrig, lives in all three lakes; smaller floating corregonine type comparable to the "Gangfisch" ("wandering fish") of Lake Constance; "Bondelle" in Lakes Neuchatel and Bienne;"Férit" in Lake Murten; bottom corregonines in all three lakes corresponding to the "Balchen" (sand corregonine) of Lake Constance, and closely related to the Féra of Lake Geneva: the "Palée".

In the course of subsequent studies, FUHRMANN arrived at a different division, and in the course of various conversations he also explained to me that he was not in a position to classify the corregonines reliably. For him the main criterion was the late maturity of the Palée and the early maturity of the Bondelle. He stated that he was unable to do anything with FATIO'S types.

In this matter we must admit that neither our investigations of fresh material nor our revisions of old museum pieces and of FATIO'S original collections have enabled us to find a useful differential diagnosis.

Here again: great degree of variability with few evident tendencies towards specialization but lacking discontinuity of the variation series except that the Bondelle type appears to be juvenile in shape and colouring, and matures early and thus is a true ecotype nanus, its characteristics in this respect being even more pronounced than those of the old Gravenches of Lake Geneva.

Let us first of all look at Lake Neuchatel.

What has been said about Lake Geneva applies almost exactly to this lake. It too is inhabited by a large sized and a small sized form of corregonine. The large one goes by the name of "Palée", the small one is called "Bondelle". From the investigations of the first sexual maturity conducted by VOUGA and MAUVAIS, we know that on the average the Bondelle matures one year earlier than the Palée but that after the first sexual maturity the rate of growth is reduced. Thus the dwarfing problem in its connection with early maturity which we already encountered in various bodies of water becomes particularly evident in this case. A prerequisite for this interconnection between Bondelle and Palée is, of course, the proof of a close relationship of the two fish which, according to the FATIO system, are assigned the value of "good species".

We have investigated considerable amounts of earlier and more recent material. We have followed the relevant literature, and have repeatedly discussed the problem of the corregonines of Lake Neuchatel with the most qualified experts of the material, Prof. O. FUHRMANN and Mr. VOUGA, Inspector General, both of whom have confirmed that it is practically impossible to tell a young Palée from a Bondelle of equal size, except during

the spawning period. It is always necessary to take note of the degree of maturity of the gonads in order to make a decision.

In 1949 DOTTRENS and QUARTIER published a biometrical sketch which is based on very thorough measurement and, in part, on a new methodical basis. Our own investigations which we are reporting for the most part took place several years ago, but I have constantly received new material in order to support my assumptions. Before discussing my own material, I would like to review DOTTRENS' and QUARTIER'S findings. The two authors limit themselves to the subject "Palées and Bondelles of Lake Neuchatel", and they forego any comparisons. On the whole they have kept to the measurements and indices used by WAGLER and myself, but they went further in the evaluation of the fin characteristics than we have by measuring the dorsal (length and base) and anal fins, while we limited ourselves to the length of the pectoral fin. Some characteristics which I designated as unreliable because they were dependent upon age were also left out of consideration by DOTTRENS and QUARTIER. On the other hand, they placed particular emphasis on all other inter-relationships arising from fin measurements and also on scale and gill raker tooth counts, and they were able to establish a formula which is supposed to enable an almost unfailing separation of the Palées from the Bondelles. Thus the two authors have confirmed that there are actual genetical differences between the Palées and the Bondelles, differences which I have in part also noted in the course of my measurements. The DOTTRENS-QUARTIER formula is, nevertheless, a somewhat cumbersome instrument for the determination

vidual fish. We do not want to discuss
ter detail here, but we would like to
e that it was used by the authors only for
n of Lake Neuchatel. We will return to this
ubsequently, and here we would only like to
t WAGLER'S rule: Palée ="Blaufelchen" (Blue
ne), Bondelle = "Gangfisch" does not find
ort in the DOTTRENS-QUARTIER formula, and that
o use the DOTTRENS-QUARTIER formula to
untenability of other "equalization efforts"
the Munich author.

Let us, however, first of all pursue the
literature and supplement it by our own
ons made in the course of the last twelve

PALEE

FATIO calls the Palée Coregonus schinzii
hus placing it right next to the Féra of
eva (Coregonus schinzii fera).

If the Palée is compared with the Féra then,
y speaking, the differences found will hardly
greater than those constantly found between
t Palées. According to FATIO the snout
Palée is somewhat more pointed than that of
. I too have occasionally found such a
ce. Then the mouth of the Féra is said to be
ightly sub-terminal position, while that of
e is supposed to be terminal. The extensive
investigated by me enabled me to establish
degree of variability in this respect. I was
find anything really typical in the shape
heads of the two large corregonines. Generally
, Palées appeared somewhat slimmer than the
They also more frequently had pointed heads,

and, in many cases, they were heterocercal, i.e. the lower half of their tail fin was larger than the upper half.

A comparative series especially investigated for this purpose resulted in the following findings:

Table bottom p.389 - German text

	Coefficient of slimness	Head length index
Palées (17 specimens)		
Féras (15 specimens)		

It is worth noting that FATD already differentiated between the normal slimmer type of Palée and a more compact Palée type, museum specimens of which I was also able to examine. On the other hand, during the height of summer, Palée swarms which are encountered out in the open water regions of the lake give every impression of acting like "floating corregonines". On August 15, 1944, I ordered a shipment of floating Palées caught above great depths in the middle of Lake Neuchatel. The group contained ten fish ranging in size from 36.5 to 44 cm., and in age from three and a half to five and a half years. The youngest ones were in the preparatory stages of their first sexual maturity. These Palées were extremely well nourished, relatively compact and fat, so that their coefficient of slimness amounted to 57.6. Their average slimness also was less than that of the Féras from Lake Geneva. It is thus clear that there are also more compact types among the Palées. Certainly none, not even the most meticulous observer, could have differentiated between the Féras and Palées on the basis of external body shapes. The closest to an external characteristic might have been certain

differences in colouring. Thus the fins of the Palées were darker than those of the Féras. The latter, for example, usually only had soot-coloured markings on the last third of their ventral fins, while the ventral fins of the Palées were dark from the very roots. This rule applied to both sexes but it was not valid in the case of juvenile individuals.

We also agree with FATIO in his conviction that the Palée of Neuchatel has a great variation range and that this large corregonine of Lake Neuchatel is quite closely related to the Féra of Lake Geneva. We, for our part, would like to add that a 100% certain identification is hardly possible.

There exist among the Palées, as has been known for some time, two "biological races" clearly differentiated by their differing spawning habits. The "Palées de bord" spawn close to the shore in November, while the "Palées de fond" do so later, right into January, and at greater depths.

In order to be able to decide whether the shore-corregonines and the corregonines inhabiting the depths differ morphologically, I ordered some twenty shore-spawning, and an equal number of depth-spawning, Palées and subjected them to a varia-statistical investigation, in order to attempt to establish a differential diagnosis. The result is not very encouraging and I am publishing it here in the form of a table.

Table bottom p.390 German text

	Palée de bord	Palée de fond
Coefficient of slimness	Max. 63.5 Min. 51.2 Mean 55	Max. 57.6 Min. 50.1 Mean 53.9
Head length index		

Size of eye

Length of caudal peduncle

Length of pectoral fin

Scale count

Gill raker tooth count

Perhaps it could be said that the Palées de bord are somewhat more compact and have somewhat smaller scales than the Palées de fond. It is, however, evident that the figures overlap to a considerable extent, and the remaining indices almost completely agree. The few cursory examinations of the rate of growth tended to show that the Palées de bord had a somewhat more rapid rate of growth than the Palées de fond.

DOTTRENS and QUARTIER in their just published study have also attempted to differentiate between the two types of Palées, but they two have not arrived at any decisive differential diagnosis. I, for my part, consider the two as ecological variants.

BONDELLE

The "Bondelle" are fish living in Lake Neuchatel, Lake Bienne, and in Lake Murten. They have, however, practically disappeared in the latter during the last few years. They are encountered in enormous swarms and play an important part in the economics of Swiss fisheries. Aside from their more juvenile proportions and their colouring, they differ but little

from the Palées. The first sexual maturity occurs in the course of the third year of life when the fish has reached an average length of 23.8 cm. in the case of the male, and 24 cm. in the case of the female. The corresponding weights are 110 g. for males, and 115 g. for females. In subsequent years the Bondelles only grow very little (to their 7th year of life to 31.5 cm. and 300 g. in the case of males, and 30.7 cm. and 300 g. in the case of females). The Bondelles checked by us showed characteristics similar to those reported by VOUGA and FUHRMANN, as well as DOTTRENS and QUARTIER in their publications. The relationship of these fish to the Palées is similar to that of the Gravenches to the Féras. On the basis of my fairly bountiful museum material, as well as from our varied statistical tables, I was able to establish that in summer, the Bondelle are fairly slim. Their gill raker teeth (average 32.5) are more numerous than those of the Palées (average about 26). The scale count is somewhat lower (83.3) as compared to 90). In all other respects the Bondelle is, however, very similar to a small Féra. It can easily be considered to be a dwarfed tribe of the Palées. The fact that it maintains "juvenile" characteristics (large head, large eyes) into advanced age would fit in to this picture as would the enlargement of the fins (pectoral fin index 13.4 compared to 12.6 in the case of the Palée, with a maximum up to 16 and 17.5). The relatively pointed snout of the Bondelle corresponds quite well to the silhouette of the Palée while the Féra and Gravenche in Lake Geneva have, on the average, as we have already noted, blunter snouts.

The Bondelle manifests a very pronounced tendency of development towards a floating corregonine, having a greater number of gill raker teeth. This appears to

be a development in the same direction as that of the "Lavaret" of Laç du Bourget, and apparently also several tribes of Féras which have begun to differentiate themselves from the main type.

Thus the inter-relationships between the Palée and Bondelle are not entirely the same as those between the Féra and Gravenche. The dwarfing process has advanced further in the case of the Bondelles of Lake Neuchatel than it has in the case of the Gravenches, and, simultaneously, certain changes have taken place indicating development towards floating coregonine characteristics. In the case of the Gravenches, these changes have to date hardly become noticeable. "Advanced individuals" having 35 and more gill raker teeth may have caused earlier authors to establish the "confususstypus" but we also have encountered Bondelles with just over 20 gill raker teeth, and Palées having more than 30. The museum specimens I examined for control purposes have fully confirmed my opinions. Various older forms which had been designated as "confusus" gave the impression of being transitory forms between the Palées and the Bondelles. Whether such intermediary forms also occur in Lake Neuchatel appears to be somewhat doubtful as far as we can conclude from the findings of DOTTRENS and QUARTIER. It is, however, certain that in Lake Neuchatel the Palées and the Bondelles do differ genetically. This, of course, does not mean that they should be considered as distinct species. After all, in the case of the homo sapiens wavy-haired and straight-haired individuals are without doubt genotypically different, but nobody would consider them to be representatives of "good" (i.e. clearly defined) species.

One further note concerning Lake Bienne:

I found two small three-year-old "Bondelles" from Lake Bienne particularly variable. I obtained them in September, 1944, from Mr. PILLOUD a fisherman from Ligerz. They were two fully matured males with spawning epidermis, both of them less than 20 cm. in length, both with long numerous gill raker teeth (39 and 40!), large eyes, and long fins. Evidently these were dwarf coregonines in whom the dwarfing tendency had developed to a particularly advanced degree. If these coregonines had been caught in Lake Thun or Lake Brienz then they would have undoubtedly been classified as "Brienzlig". In the winter of 1949-1950 I also had the opportunity to go to Lake Bienne during the spawning periods and to investigate the coregonines on the spot. The large tribe, according to my statistical data, entirely corresponds to the Palées of Lake Neuchatel. It spawns from the middle to the end of December, and, favoured by artificial breeding, it has developed very successfully. Catches of this fish include slim, as well as compact, types, individuals with terminal and sub-terminal mouths alongside of each other. Tail deformations also appear to be common. It is interesting to note that in 1948 a hermaphrodite was caughtwhich was fully matured in both sexes, and that in 1949 two hermaphrodite specimens were reported. This catch again contained several dwarf coregonines and it is certain that more of them would have been caught if the mesh of the nets had been adjusted accordingly. In this connection it should be remembered that centuries ago a dwarf coregonine ("Angelin") was reported in Lake Bienne by GESSNER.

Unfortunately I was unable to obtain any coregonine material from Lake Murten. This body of

water is so strongly eutrophied that the corregonines, with the exception of a few tiny remnants, have died out. A few museum specimens indicate the large degree of agreement with the corregonines of Lake Bienne.

To summarize:

The corregonine of the lakes at the foot of the Jura, the Palée, has a varying tendency towards dwarfing in conjunction with early maturity. The smaller Palées are called Bondelles. In addition to the usual dwarfing characteristics, they also have relatively numerous gill raker teeth and thus approach the floating corregonine type. A further systematic subdivision would not appear advisable.

As is our habit, we conclude by giving a few figures concerning variation range.

Table bottom p.393 German text

LAKES NEUCHATEL AND BIENNE

	Circumference	Head Length	Eye Diameter	Caudal Peduncle
Bondelle				
Palée				

	Pectoral fin length	Scale Count	Gill Rakers
Bondelle			
Palée			

NOMENCLATURE

We call the Balaie, Palée and "Pfarrig", as well as the Palchen and other similar large-sized corregonine forms

Coregonus lavaretus L. nat. jurassica,
ecotype primigenius

The Bondelle and other designations for the small corregonines, "Ferit"

Coregonus lavaretus L. nat. jurassica,
ecotype nanus.

E. LUNGERN LAKE

Lying 657 m. above sea level, Lungern Lake -- just like Klontal Lake -- is a true mountain lake which today also serves as an artificially dammed lake for the production of hydroelectric power. Its surface area at one time measured .87 sq. km., its volume .0146 cu. km. Its greatest depth was reported at 32.9 m., its mean depth 17 m.

It is not quite easy to decide whether Lungern Lake should be considered as one of the old original corregonine lakes or whether its corregonine population is the result of re-stocking in more recent times. It is not one of the 16 Swiss lakes enumerated by FATIO in 1890. On the other hand, H. FISCHER-SIGWART has, according to the testimony of Dr. ETTLIN from Sarnen, announced in 1890 that now and then, but very infrequently, a dead corregonine could be observed floating at the surface of the water, but that no living corregonines had, up to that time, been sighted. On December 1, 1890, a corregonine from Lungern Lake was said to have been sent to FATIO. In 1904 Dr. FISCHER-SIGWART received another specimen which is still preserved in the museum at Zofingen. FISCHER emphasizes the similarity to the Albock of Lake Thun, and particularly points out that the mount was terminal. The jaw is described as reaching far to the rear. The length of the fish was 30.5 cm. The snout, which reached up to the pupil, was reminiscent of the Lavaret in Lac du Bourget. FATIO himself refers to the case in the "Fischereizeitung" (Fisheries Journal) in 1897. He notes that the Lungern Lake corregonines examined by him appeared to be particularly close to the albock of Lake Brienz (Coregonus wartmanni alpinus), but showed considerable differences from the corregonines of Sarner Lake, which

must be considered as "Balchen".

For almost ten years after that nothing further was heard concerning corregonines in Lungern Lake.

On July 29, 1909, on the initiative of Mr. HOFER, Fisheries Supervisor at Meggen, experiments using six floating nets having a mesh of 30 mm. resulted in a catch of 18 beautiful corregonines, weighing from 120 to 530 g. each, with the average weight being 364 g. In other words, these were large corregonines. In 1912 the experiment was repeated, this time using bottom nets, and the results were by far better. One set of bottom nets (two or three nets) within a single day resulted in a catch of 30 fish. Nevertheless, it appears that none of the local net fishermen showed any interest in these catches, for corregonine fishing was soon forgotten once more.

In WAGLER'S great studies dealing with the Central European corregonine, there is no mention of the corregonine of Lungern Lake. On the other hand, this fish is mentioned in a study by L.S. BERG, under the name Coregonus lavaretus wartmanni nobilis, i.e. as "Edelfisch" ("Noble Fish") of Lake Lucerne. In FATIO'S original collection (at the Geneva Museum) there merely is a specimen with the inscription "Coregonus wartmanni nobilis from Lungern Lake" and it probably represents Dr. ETTLIN'S already mentioned individual. It is said that around 1912 Mr. HOFER, the Fisheries Supervisor, introduced corregonine fry from Lake Lucerne -- probably Balchen -- into Lungern Lake, but I was unable to obtain any further details concerning this. In the last few years experimental catches conducted by Mr. GOTTFRIED HOFER, a Master

Fisher from Oberkirch, were able to establish the presence of a considerable coregonine population which, in the meantime, has become further modified through the introduction of locally obtained fry as well as stocking with fry from Sempach Lake and Zuger Lake. Thus Lungern Lake today probably contains a form of coregonine, which, being a mixtum compositum, is not particularly interesting genetically, whose present status should, however, be recorded here.

Material investigated: 228 specimens from various zones caught at various times. All specimens were two, three, or four years old.

General characteristics: Beautiful silvery colouring, fairly pointed head with well developed usually strongly soot-marked fins, basic colour bluish gray, fairly slim outside of the spawning period.

Length: Minimum 23 cm.
Maximum 37.5 cm.
Mean length of the age groups
2-year-olds 24.9 cm.
3-year-olds 29.0 cm.
4-year-olds 31.3 cm.

The coefficient of slimness is subject to considerable fluctuations but is only very exceptionally under 50 (45.5 in the case of the female measuring 32.5 cm. which had particularly small eyes and also did not fit in the general pattern in other respects, and therefore could have represented a special tribe, as well the few isolated instances in which it amounted to 49.5). On the other hand, however, particularly compact specimens having a coefficient of slimness of more than 60 were also encountered, but in these cases a swelling of the swimming bladder must be taken into consideration.

The head length in most cases amounted to 16-18%. The largest individuals had, as is usual, the smallest

heads:

	Length	Head length index
Female	33.5 cm.	15.2%
	35.3 cm.	15.7%

One of the very smallest specimens had the largest head:

Male	23.4 cm.	23.1%

The eye size only very infrequently drops below 4%, and in exceptional cases reaches 4.9 and 5%, and even 6%. The mean is somewhere around 4.4%. The Lungern Lake corregonines thus appear to have fairly large eyes.

The length of the caudal peduncle is subject to considerable fluctuation, but on the average it is quite prominent:

Minimum	5.8
Maximum	10.1
Mean	7.8

The length of the pectoral fin has been recorded at about 14%. The fluctuations are not very great. Two-year-old ones definitely have relatively shorter fins than four-year-old ones which once more proves that with advancing age the rate of growth of the fins is greater than that of the remainder of the body. The only specimen noteworth in this respect was a relatively small four-year-old, i.e. evidently a retarded female, which, having a body length of 29.1 cm. achieved a pectoral fin index of 16.7, while a particularly rapid growing two-year-old one, measuring 26.5 cm. had pectoral fins amounting to but 12.1% of the body length.

Scale count varied from 80 to 93.

Concerning the number of gill raker teeth, we noted the following figures:

Minimum 28 teeth on the 1st gill raker arch
Maximum 41 teeth on the 1st gill raker arch
Mean 34.3

with only a single individual having fewer than 30, and the vast majority falling into the categories 32-35.

Thus the corregonines of Lungern Lake were shown to be close to the Primigenius type, probably the so-called "Balchen" of Lake Lucerne. They are also close to the Albocks of Lake Thun, but as a result of a different food supply, and due to the particular conditions prevailing in an artificially dammed lake, their growth is somewhat lagging behind the above-mentioned types. Nevertheless, a very good rate of growth is maintained during the first and second years of life. The two-year-old corregonines from Lungern Lake are almost equally as large as the so-called "Sandfelchen" ("Sand corregonines") of Sempach Lake and Lake of Zurich. As far as can be judged from the oldest available reports, the "original corregonine" of Lungern Lake, if we can speak of such a fish, had similar properties. It is interesting that in spite of the high altitude of the lake, and in spite of temperature conditions and a fairly long-lasting continuous ice cover, and in spite of the artificial damming of the lake which leads to a radical annual lowering of the water level, there is no indication of a development towards dwarfed growth, neither in general nor in the case of individual tribes. We encountered no dwarf corregonines whatever.

The corregonine of Lungern Lake spawns in the third and fourth year of life during the winter, usually not earlier than the end of January, and occasionally under ice. Artificial breeding is only possible in the years in which the ice cover is correspondingly delayed.

The yields have, in the course of the last few years, been quite good. Four fishermen using nets are at present engaged in their trade on this small body of water. One of these fishermen keeps exact records. His summer catches using floating and

bottom nets frequently brought daily catches of 100 to 150 fish, occasionally more than 170. In 1944 he caught 5,241 fish. The other three fishermen probably caught an equal number between them, so that a total yield of the lake during a summer season is approximately 10,000 corregonines. To this we must add the not inconsiderable winter spawning catches which can be achieved in suitable years.

NOMENCLATURE

The corregonine of Lake Lungern is to be designated as follows:

Coregonus lavaretus L. nat. riusensis, ecotype primigenius.

Table bottom p.397 German text

LUNGERN LAKE

Circumference Head length Eye diameter Caudal Peduncle

Length of pectoral fin Scale count Gill raker teeth

F. LAKE LUCERNE

Lake Lucerne is one of our largest lakes, particularly because of its considerable volume (11.8 cu. km.) which is the result of a mean depth of 104 m. (maximum depth 240 m.). The area of this very irregularly shaped basin has been calculated as being 150 sq. km.

The abundance of fish in Lake Lucerne has already been known from the earliest times. First the monasteries, and later the fish market at Lucerne, accounted for the greater part of the fish caught in the lake. From occasional reports and records we have some indication of fishing conditions in bygone centuries. One of the earliest Chronicles is JOHANN LEOPOLD CYSAT Assistant City Clerk of Lucerne who, in 1645, devoted a monographic study to the lake. We found the following

section particularly interesting: "And different marvelously good fish are to be found within it." The 10th chapter of CYSAT'S study deals with "Balchen" "Edelfisch" "Weissfisch" and "Eglin" and is evidently based, to a considerable extent, on the then recognized authority of CONRAD GESSNER from whose "Fischbuch" ("Book of Fish") various passages have been copied practically verbatim, but there are also indications that CYSAT had specific sources having a special knowledge of Lake Lucerne. These are supported by the following data which we briefly summarize here:

In Lake Lucerne the small coregonines are called "Nachtfische" ("Night fish"). They were only slightly longer than a human figure and they were caught by means of lake bottom nets at 40 to 50 fathoms. The "Noble Albulen" also called "Edelfisch", ("Noble fish") was much larger. It lived closer to shore. Around 1645, fishermen differentiated between the "Krautbalchen" (Weed balchen) "Steinbalchen" ("Stone balchen") and "Schwemmbalchen" ("Aluvial balchen"). The latter weighed as much as nine pounds. The fact that in 1650 "close to 1,000 pounds" of Balchen were sold on a single day is the indication of the abundance of fish during those years. It appears probable that the fish in question was not a "Balchen" in the present-day sense of the word, since the "Balchen" were only caught during the spawning period, while the above record was said to have occurred in August. Probably all coregonine species, both large

and small, young and old, were occasionally designated by the collective name "Balchen".

From newer, and most recent, periods we have a whole series of special studies dealing with the corregonines of Lake Lucerne. We only would like to mention: W. NUFER, G. SURBECK, A. BIRRER and W. SCHWEIZER. All these authors based their studies on the VIKTOR FATIO system.

Of particular significance in this connection are the monographic studies devoted to corregonines by A. BIRRER and W. SCHWEIZER in the years 1935 to 1938. These publications contain a considerable collection of material as well as a statistical digest of this material. When we compare our own measurements and counts with BIRRER'S and SCHWEIZER'S data, then the large measure of agreement between the two becomes apparent, and a revision of these studies would therefore not seem advisable. Nevertheless, we should fundamentally state our position concerning the justification of uncritically accepting FATIO'S systematic principles and we should decide whether it might not be necessary to find new ways as we have in the case of Lake Thun. The principal question in this respect is whether three well-known corregonines of Lake Lucerne should figure as separate species in the system or whether they only represent ecotypes which have differentiated themselves from each other on the spot.

On the basis of our own years of acquaintance with the corregonines of Lake Lucerne, we have understanding for the fact that separation into "Balchen" "Edelfisch" and "Albeli" (Weissfischli)("Little White Fish") has developed in analogy to the common names

used by fishermen. It is easier to differentiate between these three types than, for example, between the two old corregonines of Lake Geneva, Féras and Gravenches, or between bottom albocks and the floating albocks and the Brienzlig of Lake Thun. To date, the usual procedure was to select typical specimens from an abundant catch or to have them selected by the fishermen. These specimens then showed considerable agreement in many of their characteristics, and the picture changes entirely. We review the various fish of Lake Lucerne without prejudice and statistically work out our observations. In such a case we suddenly realize that next to typical forms there are also uncertain ones, so to say "Transition specimens" which fit into neither one nor the other of the ideal pictures created by us. It would not be difficult for us at all to compile a single series practically without gap, from "Balchen" to "Edelfische" on the basis of but a few catches from Lake Lucerne, in particular if we include both young and extremely young specimens. The same applies to an even greater measure for the relationship between the "Edelfisch" and "Albeli".

The genotypical differences are certainly by no means constant, and certainly many properties which we up to now attempted to utilize for the characterization of the individual types are caused purely phenotypically, that is to say, directly by environmental factors such as habitat, nutrition, development conditions of the fry, temperatures, and, perhaps, by the degree of maturity and age. In our subsequent remarks, we will attempt to emphasize these points.

The material investigated by us comprises 180 corregonines from Lake Lucerne. Of these, 49 can, without question, be categorized as "Weissfischli", 64 as "Edelfisch", 25 as "Balchen". In the case of

42 specimens, the classification is more difficult. The fish originate from entirely different parts of the lake and have been caught at various seasons of the year.

Under the label "Balchen" the museum at Basle features a "typical" specimen contributed by HOFER in 1906, with more than 30 gill raker teeth, 47 cm. in length, and six years old, in addition to that a but two-year-old specimen with 30 gill raker teeth: coefficient of slimness 48.1%,

head. length	17.9%
size of eye	4.48%
length of pectoral fin	13.1%

that is to say, old juvenile characteristics which would move the fish very close to the young "Edelfisch" or perhaps even to the "Weissfisch".

The situation becomes even more critical in the case of the so-called "Blaufelchen" ("Blue corregonine") which have been caught near Stans and in Alpnach Lake. The proper classification of these fish is more or less a matter of "intuition". Their gill raker tooth count fluctuates from 34 to 38, the mean being 36. Their body proportions on the whole correspond very closely to those of the "Edelfisch" but their spawning period is during the end of December, and they spawn fairly close to the surface. The corresponding juvenile fish, aged two to three years -- still immature -- are frequently caught in "Weissfisch" nets. Their colouring is frequently bluish and this has now caused some fishermen to call them "Blaufelchen" ("Blue Corregonines").

COEFFICIENT OF SLIMNESS

According to our own measurements, the relative circumference varies within even wider limits than those established by BURGER-SCHWEIZER on the basis of

their investigations. Our figures ranged from 44.1 to 62.4 with a mean at somewhat under 50.

According to BIRRER-SCHWEIZER:

Balchen	Maximum 59.5 Minimum 47 Mean 54.06
Edelfisch	Maximum 56.8 Minimum 44.3 Mean 50
Weissfisch	Maximum 49.3 Minimum 45.7 Mean 48.65 (after spawning period 45.84).

In connection with these figures obtained by the two authors, it should be noted that they are misleading to the extent that they measured almost only young "Weissfischli" and almost exclusively old "Balchen", but that, as is generally known, and specifically confirmed by BIRRER-SCHWEIZER themselves, the relative circumference increases with age.

We have also investigated young and therefore slim "Balchen" and compact, old "Weissfischli", and as a result we came to the conclusion that the coefficient of slimness is of little use in differential diagnosis except when material having exactly the same age is being compared. Even in such a case we would have to examine whether -- aside from age -- the rate of growth did not influence the slimness or compactness in the sense that larger, more rapidly growing specimens soon appeared plumper and more compact than smaller ones whose growth was retarded.

RELATIVE LENGTH OF HEAD

What has been said above also applies here.

According to BIRRER-SCHWEIZER:

Balchen	Maximum 17.5 Minimum 15.5 Mean 16.44

Edelfisch	Maximum 17.0 Minimum 16.0 Mean 16.26
Weissfischli	Maximum 20.0 Minimum 14.5 Mean 17.9

The largest of the "Weissfisch" investigated by us had the smallest head, so this criterion too was proven to be dependent on age. The juvenile "Balchen" and "Edelfisch" also definitely have large heads.

SIZE OF EYE

Our material exhibited very great fluctuations: 2.1-5.31.

According to BIRRER-SCHWEIZER:

Balchen	Maximum 3.6 Minimum 2.7 Mean 3.05
Edelfisch	Maximum 4.1 Minimum 2.8 Mean 3.27
Weissfischli	Maximum 5.2 Minimum 3.8 Mean 4.3

Eye sizes of less than 3% appear in our series only in the case of large and extremely large fish (Balchen measuring from 45 to 60 cm.). Size of over 5% have been noted in the case of 19 to 22 cm. long small coregonines. A 27 cm.-long "Weissfisch" aged 5 years, had an eye diameter of only 3.7%. A young "Balchen" measuring 26.8 cm. had an eye diameter of 4.48%. Thus the size of the eye is not a useful species criterion.

LENGTH OF CAUDAL PEDUNCLE

This characteristic was not taken into consideration by BIRRER-SCHWEIZER, who measured the "height" of the caudal peduncle instead, which, in turn, was not measured by us.

Our figures show that the length of the caudal peduncle fluctuates within fairly wide limits.

In all the forms investigated by us, no direct relationship between this and the age of the specimens investigated could be determined.

Balchen	maximum 9.0 minimum 5.14 mean 7.5
Edelfisch	maximum 11.4 minimum 6.6 mean 8
Weissfischli	maximum 9.4 minimum 5.7 mean 8

Perhaps it is noteworthy that only in the case of the "Edelfisch" is the proportion ever greater than 10%, but even here such long-tailed specimens are the exception.

LENGTH OF PECTORAL FIN

According to BIRRER-SCHWEIZER the following figures apply:

Balchen	Maximum 17.5 Minimum 12.0 Mean 13.6
Edelfisch	Maximum 15.1 Minimum 11.4 Mean 13.01
Weissfischli	Maximum 15.5 Minimum 11.5 Mean 13.44

All figures obtained by us lie within this range,--With the older age groups clearly closer to the maximum and the younger ones close to the minimum. Here again the pectoral fin grows relatively more rapidly than the remainder of the body with advancing age. This characteristic cannot be used for purposes of differential diagnosis.

SCALE COUNT

As we have already noted, the relative size is most clearly expressed when we determine the number of scales along the lateral line. We can thus, for

example, uncover the contradiction inherent in NUFER'S study, who claims that the "Balchen" has "large" scales and the "Weissfischli" small ones, while, in fact, there are 82 to 99 scales on the lateral line of the "Balchen" and only 78-88 on that of the "Weissfischli".

According to BIRRER-SCHWEIZER we should note the following scale counts:

Balchen	Maximum 97 Minimum 75 Mean 88.2
Edelfisch	Maximum 101 Minimum 80 Mean 91.7
Weissfischli	Maximum 92 Minimum 70 Mean 82.3

In contrast to the other criteria, this appears to be a characteristic which could be utilized for the "Weissfischli" has, on the average, many fewer scales than the large corregonines.

This is also apparent from our figures, with the fluctuations occasionally being even somewhat greater than those determined by BIRRER-SCHWEIZER.

Balchen	Maximum 102 Minimum 77 Mean 89
Edelfisch	Maximum 10 Minimum 7 Mean 88
Weissfischli	Maximum 93 Minimum 69 Mean 84.5

This tends to blur the difference between the "Edelfisch" and the "Balchen" and thus the scale size too is a doubtful criterion for the differentiation of the large corregonines, and its validity in the case of small corregonines is limited to mean values based

on large populations.

GILL RAKER TEETH

This characteristic is, as is well known, considered particularly significant for purposes of "species diagnosis". The following are BIRRER-SCHWEIZER'S figures:

Balchen	Maximum 30 Minimum 23 Mean 25.5
Edelfisch	Maximum 41 Minimum 32 Mean 35.5
Weissfischli	Maximum 42 Minimum 35 Mean 38.7

According to this, the number of gill raker teeth of the first arch of the Balchen is considerably smaller than that of the Edelfisch, which, in turn, tends to have a somewhat lower gill raker tooth count than the"Weissfisch".

More material on the whole confirmed these findings:

Balchen	Maximum 31 Minimum 20 Mean 24.4
Edelfisch	Maximum 42 Minimum 31 Mean 36.0
Weissfischli	Maximum 42 Minimum 35 Mean 37.4

The large winter-spawning coregonines of Stanser and Alpnach Lakes have gill raker tooth counts of 29-38 and can, in a sense, be considered intermediate connecting links between the "Balchen" and "Edelfisch", if we do not wish to assume that the various re-stocking measures have caused the appearance of a new type in the lake.

On the basis of the figures compiled here

we cannot establish any other diagnosis for the coregonines of Lake Lucerne than for the other coregonines. A basic type of average characteristics has differentiated itself into two biologically different forms. Thus the floating coregonine "Edelfisch", on one hand, and the bottom coregonine, "Balchen", were created, and they are, to this very day, connected to each other by intermediate forms. From the "Edelfisch", or perhaps from the basic type, an early maturing dwarf tribe has branched off, and it, in turn, appears to be in the process of splitting up into biological races. The fact that the various tribes of Lake Lucerne are more closely related to each other than they are, let us say, with the fish inhabiting Lake Constance, is evident from common features characterizing the coregonines of Lake Lucerne: relatively numerous and long gill raker teeth, relatively large eyes -- similarities which, though they are less obvious than differences in body proportions are, since they are genotypically caused, more meaningful for genetical purposes than growth characteristics would be.

The living habits of the coregonines of Lake Lucerne is quite well known through previous publications. In particular we would like to refer to BIRRER-SCHWEIZER'S, SURBECK'S and WAGLER'S studies. For the sake of completeness, and in order to obtain a certain basis for comparison with the coregonines of other lakes we have compiled some of the points.

NUTRITION

We know practically nothing concerning the year-round nutrition of the "Balchen". BIRRER-SCHWEIZER have investigated spawning fish only. It is remarkable

that in the stomachs of these fish, remnants of plankton crustaceans predominated and lake bottom nutrition (insect larvae and pisidii) were only found in isolated instances. The authors assumed that depending on the season of the year, they consumed alternately more plankton or more bottom nutrition. Our own findings confirmed this opinion.

The "Edelfisch" is predominantly a plankton eater. In springtime it consumes more copepods, later on Daphnia, and finally deep-water crustaceans like the Leptodora and Bythotrephes. In summer this is supplemented by pupae of chironomides. The diet of the "Weissfischchen" ("Little White Fish") is similarly composed. According to the tables compiled by BIRRER-SCHWEIZER copepodes predominate in winter, Cladocerae, in particular Daphnia, in summer, and in autumn they are joined by chironomides.

In the case of the "Weissfischli" of Alpnach Lake, the composition of the menu varied considerably with the "larvae of the Corethra" (Sayomyia plumicornis) clearly predominating at times. There also were oligochaeda, ostracoda and pisidii. In the course of our own investigations of stomach contents of white coregonines of the Hergiswil region, we found specially great amounts of the deep-water crustaceans, Bythotrephes, as well as Bosmina. In other cases we noted a quite considerable proportion of lake bottom nutrition (pisidii and insect larvae). These were particularly encountered in the case of "Sommerweissfischli" ("Little summer white fish") inhabiting the depths. Near Beckenried, we repeatedly caught "Weissfischli" which had consumed lake bottom nutrition exclusively, and thus, by their nutrition, corresponded to the type Profundus.

It is apparent that, on the whole, the nutrition of the various coregonines of Lake Lucerne shows few significant differences. One thing is certain, and that is that the small and large coregonines, swarms of which head towards the relatively shallow Lucerne Basin in spring and summer, come there in order to feed on the pupae of the various water insects which, at that time of year, form their main nourishment. Here the so-called "Hegenen" "Weissfischli" and juveniles of the large coregonine species can be caught with their stomachs filled to the bursting point.

REPRODUCTION

The various forms of Lake Lucerne coregonines show exceptionally great differences in their spawning habits.

According to BIRRER-SCHWEIZER, FATIO, and others, we should record the following spawning conditions in the form of a table:

Type	Spawning period	Spawning place
Balchen	November 18 to December 9 in the so-called "Inner" lake somewhat later than in the so-called "Outer"	Rocky shorelines Surface deposits
Edelfisch	End of July to beginning of September	At depths of 100-200 m. on the bottom of steep slopes
Weissfisch	1st summer: July-August 2nd Winter: October-December	Near the shore close to raised parts of the lake bottom, moraines, depths of the lake

On the basis of our own experiences we would like to make some corrections or amendments: the "Balchen" spawns in the "inner" lake up to Christmas, occasionally even longer. The "Edelfisch" may, in some years, reach maturity as early as the middle of July, as can the "Weissfischchen" ("Little White Fish"), which, on the

other hand, may still be encountered mature in January, and may be caught in depths ranging from 50 to 60 m. There are but very slight differences between "summer spawners" and "winter spawners" and these visible differences cannot be recorded statistically. We have attempted over a period of years to establish the differences, and we were unable to do so. The fact that more coregonines caught at lake depths are often strongly bloated and, in their external appearance, are reminiscent of the "Kilche" or the "Kropfer" of Lake Thun is not at all surprising. Some populations appear to have gotten used to life in the depths, although their gill raker apparatus marks them as typical "Albeli" they show ecological characteristics of the type profundus. They usual spawn at depths ranging from 70 to 80 m,, occasionally even deeper. Their summer spawning activity and their preference for nourishment from the lake bottom should be particularly emphasized.

The "Weissfischchen" of Alpnach Lake are, as far as we have been able to determine to date, invariably winter spawners of even more compact stature than the others and a somewhat broader caudal peduncle. During the last few years their numbers have decreased considerably, and they have given place to the so-called "Blaufelchen" ("Blue coregonine").

GROWTH

We are lacking precise orientation concerning the growth of the "Balchen". We only were able to examine two immature two-year-olds, and all the others available to us were older specimens. BIRRER-SCHWEIZER had, in the main, only four-year-old and older spawning fish at their disposal.

We do not consider the methods of DAHL-LEA, who determined the length of the individual age groups

indirectly from the breadth of the growth rings on the scales as being very variable. Our reason for doing so was explained in greater detail on p.155 of the first article.

On the whole, our figures correspond well to those published by BIRRER-SCHWEIZER and in some aspects they complement them. It should be noted that in their investigations of spawning fish, BIRRER-SCHWEIZER record five-year-old ones as the youngest (only in some isolated years four-year-old ones came to the spawning places, but the main contingent consisted of five and six-year-old ones.). Accordingly, the "Balchen" would appear to mature late in life. The mighty growth from 20.8 cm. during the third year to 30.37 cm. in the fourth year falls into the period during which the gonads are still entirely immature. The fish even grow far beyond the average of their age group, in isolated instances all the way to 43.5 cm. in the fourth year. Thus the interconnection between the rapid rate of growth with the retarded spawning is made quite evident. Generally speaking, there is a considerable"growing apart" of the fish. This is typical of litoral types.

Similar observations were made with the "Edelfisch". A majority of those participating in the spawning are four and five-year-old. The most rapid growth takes place in the periods preceding the first spawning maturity, but we have also encountered mature "Edelfisch" weighing but 120 g., and it was very difficult to tell them from "Sommeralbeli" ("Summer albeli") maturing at the same time.

Just how much "Edelfisch" can grow apart is proven by the results of an investigation conducted at Meggen in the course of which I attempted to pick average, largest and smallest fish from a day's catch in order to determine the youngest and oldest age groups participating in the spawning. The result was the following paradoxical distribution:

Table bottom p.407 German text

Length in cm.	1st year	3rd year	4th year	5th year	6th year

It is evident how very individual the "growing tendency" is; the oldest were not the largest! Among the four-year-olds the body length varied from 25 to 40 cm. Probably this great variety in the rate of growth is due to the fact that some Edelfisch achieve maturity during the third year, others only in the fourth, or, perhaps, not until the fifth year of their life. The theory that they were subjected to very different nutritional conditions, i.e. that some were subject to starvation while others had an immoderately large food supply, appears improbable.

In the beginning the rate of growth of the "Weissfischchen" remains within entirely normal/and respectable limits. Let us compile the sizes of the first three age groups as calculated by BIRRER-SCHWEIZER according to the DAHL-LEA method:

Table top of p.408 German text

	1st year	2nd year	3rd year
Balchen			
Edelfisch			
Weissfischchen			

By a direct method the authors found the average length of the three-year-olds to be 20.37 cm. in the case of a first series, and 20.35 cm. in the case of a second series. We too arrived at considerably higher mean values than those contained in the calculation. Our "Weissfischchen" hardly lagged behind the large coregonines up to the third year. We recorded two-year-old ones measuring 17 to 19 cm. in length. After that their growth becomes considerably retarded as is shown in the following table:

Table bottom of p.408 German text

	4th year	5th year
Balchen		
Edelfisch		
Weissfischchen (Kreuzrichter)		
Weissfischchen (Weggis)		

Early maturity appears to be the direct cause for premature cessation of growth. After the terrific effort of maturing, the fish no longer appears to be capable of considerable growth. It also matures in the subsequent years: the sex hormones assert their predominance over the growth hormones, thus resulting in the dwarfing phenomenon.

MIGRATIONS

One chapter in the biology of the coregonines of Lake Lucerne which to date is still insufficiently explained is the movement of the swarms. It is certain

that many coregonines, particularly "Weissfischchen" appear in great numbers in the lake near Lucerne in spring and summer and are decimated there by numerous anglers. According to the reliable testimony of Mr. NAEFLIN, a fisherman from Brunnen, there are repeated occasions when near Gersau, and even in Urner Lake, white fish have been caught and are being caught which have broken fish-hooks stuck in their jaws. Since the lake basin in the vicinity of Lucerne is the only place in which coregonines are caught with hooks, it can be assumed with certainty that the "Weissfisch" again wander back long distances all the way to the innermost part of the lake. The "Edelfisch" also undertake large-scale wanderings. In the summer months they disappear almost completely from the area of the "outer lake" and move to deeper spawning places near the Burgenstock and in the Gersau Basin all the way to Urner Lake, only to reappear in the "outer lake" again in October and November, which months usually are marked by the best catches in the "outer lake". Whether all swarms participate in these migrations to an equal degree and how these horizontal movements combine with vertical ones is hardly known. Some experienced fishermen report that in winter, and all the way into spring, the "Edelfisch" live out in the open water region of the "front lake" where, provided the proper tackle is used, they can be caught in satisfactory numbers.

In spite of all efforts, I was able to obtain but little information concerning the living habits of juvenile "Balchen". The Balchen of Lake Lucerne, unlike the "Sand coregonines" of the lakes of eastern Switzerland, are not inhabitants of the lake shore. I was assured

that during the first quarter of the year, numerous young Balchen could be caught together with "Edelfisch" in so-called floating nets. I only obtained two such specimens for investigation.

THE INFLUENCE OF STOCK INTRODUCED FROM OTHER LAKES

G. SURBECK (1920) has stated his position in the matter of the problem "species continuity after the introduction of alien fry", and concerning the possibility of assimilation of alien fry to locations after a few years, in an interim report and a detailed study which he bases principally upon the "Ballen" of Sempach Lake, and the "Balchen" of Lake Lucerne. The question raised by him is of fundamental significance and must also be dealt with here. In 1900, when the "Balchen" population had dropped to an unusual low, millions of "Ballen" fry were obtained from Sempach Lake and introduced into Lake Lucerne in the subsequent years in order to aid the "Balchen". A few years later the fishermen of Lake Lucerne felt that the number of "Balchen" had increased considerably, but they stated at the same time that the new populations were composed of different types, namely of Sempach Lake "Ballen". But these Sempach Lake coregonines were, in fact, the descendants of millions of Balchen of Lake Lucerne introduced into Sempach Lake from 1895 to 1902, when the latter's coregonine population had almost died out. We now find that if we go back to FATIO'S investigations, that originally there was a considerable difference between the Sempach Ballen (Coregonus suidteri) and the Lake Lucerne Balchen (Coregonus schinzii helveticus). The variation range for the number of gill raker teeth on the first gill arch for the coregonus suidteri was

considered to be 38-42, and for the Coregonus schinzii helveticus, 23-28. Thus it should have been possible without any difficulty to tell the old Lake Lucerne Balchen from the supposedly Sempach Ballen. SURBECK had the fishermen forward both the old and the new from from Lake Lucerne, and finally also the original forms as they existed around 1920 in Sempach Lake, and then investigated them. He found:

Even today's "Ballen" of Sempach Lake no longer corresponds to the Coregonus suidteri described by FATIO. The numer of gill raker teeth has decreased considerably, and today it ranges between 30 and 36. It seems very strange, but the gill raker teeth counts given by FATIO for the "Balchen" of Lake Lucerne also no longer applied. Even in the supposedly"old" form, the number of teeth appeared somewhat greater. From this, SURBECK concluded that the Balchen of Lake Lucerne which originally were equipped with a smaller number of gill raker teeth developed a denser gill filter after their transplantation to Sempach Lake. In the course of the subsequent transplantation of the Sempach coregonine into Lake Lucerne the number of tiny gill raker teeth was again reduced. Unfortunately, SURBECK'S findings were based on a very small number of individuals and his average figures and frequency values must be accepted with very great care. It is entirely possible that these differences may have evened themselves out if the calculations were based on a greater number of specimens. It has been shown over and over again that the variation limits of individual forms become greater when the amount of material investigated increases. As a result it frequently happens that the characteristics of one form overlap those of another, in other words that a seemingly discontinuous variability in the final analysis

is proven to be continuous. What is of importance in SURBECK'S finding should, however, be particularly emphasized here: in the course of the revitalization of impoverished, almost died-out stocks, it is possible to obtain satisfactory results within a few years. The new forms thus created can easily be told from the old ones and they show certain similarities to the population of their original lake, but, on the other hand, they also soon appear to adopt characteristics imposed upon them by their new habitat. This, once again, proves the great pliability of the coregonine group. The idea that changes are the result of crossings of old and new stocks is, on the whole, rejected by SURBECK. The advanced impoverishment of the old stocks makes it most improbable that they could significantly affect the new population through cross-breeding.

THE STATE OF HEALTH

It is also worth noting that crippled and stunted tail fins so frequently found in other lakes are practically unknown in Lake Lucerne. On the other hand, Henneguyia zschokkei cysts are occasionally encountered, and during the last few years an unusual disease of the edge of the fins has attacked the Albeli, the end of whose fin rays tend to become brittle and drop off. To date the exact nature of this disease has not been discovered.

COREGONINE FISHING IN LAKE LUCERNE

Ever since ancient times the coregonine have, by far, been the most important object of the efforts of the fishermen of our original cantons. The "outer lake" west of it the "Nase" (in the vicinity of Burgenstock/Vitznauerstock) bases its fishing economy primarily upon the small coregonines (Albeli or

Weissfischchen), while for the fishermen of the "inner lake", the "Edelfisch" is the main catch.

Until the end of the 19th century the Albeli was caught in accordance with ancient tradition with fine meshed drawing nets which could also be used on underwater slopes. Evidently around that time complaints were heard concerning the decrease in the coregonine stocks and the competent authorities issued regulations prescribing a minimum mesh of 30 mm. This immediately stopped the drawnet fishing of Albeli since the small fish were, without exception, able to slip through the drawnets. In 1895 special "Albeli nets" having a mesh of but 24 mm. were allowed, but their use was restricted. They could only be used as bottom nets at depths of at least 20 m. In the period from October 1st to December 31st, which was officially designated as the spawning period, the prescribed nets had to have a minimum mesh of 30 mm. After the new year, the Albeli fishing was again intensified. The Albeli nets were very popular during the subsequent years. In the "outer lake" around 1910, no less than 500 nets were used to catch these small coregonines. The yield was estimated at around 20,000 Swiss francs, even though the kilogram sold for only 1.60 to 2 francs, and during the main catching season, even considerably less. Since the little fish weigh 70 g. on the average, it is plain what enormous numbers were brought up from the lake in those days. Nevertheless, there was hardly any artificial breeding. Conservation was limited to the suspension of fishing using fine mesh nets during the protection period. Since the latter only coincides with a part of the spawning period, Albeli, which are mature for spawning are even today caught during August and September. The "Weissfischchen" which spawn in summer

thus get no protection whatever through the closed season.

And what about present-day catches? It is difficult to compare them to those of earlier years since we have little useful data concerning coregonine stocks of by-gone years.

One bit of historical information is, nevertheless, of interest:

The fishermen of the town of Stansstad (38 members of the St. Nicholas Fraternity) in the 12th and 13th century were obliged to supply 4,300 "Weissfisch" and 30 "Balchen" annually to the monastery at Engelbert, provided that these were real types (in other words tens), then we can assume that the total catches of those days roughly corresponded to present-day ones.

For the report year 1932/33 the fisheries districts of Lake Lucerne show 19,589 kg. of Weissfischli for the "outer" lake alone. The "Balchen" catches for the years 1932-1937 amounted to 1300 to 2600 kg. annually, and those of "Edelfisch" from 13,000 to 18,000 kg. We will return to the data of the official statistics and we have merely given a summary of the yields in order to obtain a comparison with the legendary yields of by-gone days.

It is certain that during this century there have been repeated complaints concerning the periodic decrease in the number of "Weissfischchen". Only a few years ago there were again complaints about poor catches. In this connection, the increasing use of hooks, i.e. the so-called "Hegenen" in the basin near

Lucane was considered particularly harmful for even small and very minute coregonines are caught on the hooks, and they cannot be returned to the water. We too gained the impression that this was an irresponsible method of "mining" the lake, which would result in untold harm in the long run. In the most recent period, the catches of the angle-fishermen have again decreased. There are differences of opinion concerning the coregonine stocks around the middle of this century. In 1949-50, experiments were undertaken for the first time in the artificial breeding of the Albeli. The results of these experiments are eagerly awaited.

The "Edelfisch" was called the professional fisherman's real bread and butter, both in the past and today this applying primarily to the "inner" lake. The yields obtained by the fishermen there are considerable. They use floating nets out on the open lake at depths of 5 m. and more. In former decades drawnets were used, but ever since the middle of the 19th century, the fishermen of Gersau, Buochs, etc., began using lake bottom depth nets near the spawning grounds of the Edelfisch at depths varying from 80 to 200 m. There, near rocky underwater slopes, or close to the surf mounds of streams, they allowed the nets to stand for one or several nights, with excellent results. But towards the end of the eighties of the last century a decrease in the catches could be observed, and, simultaneously with it, a considerable increase in the size of the individual fish. This also applied to "Edelfisch" caught in floating nets, the average length of which had increased considerably. If previously floating nets having 32-35 mm. mesh had been used, then the mesh could now be increased to

38-42 mm., but the complaints concerning the decrease of the "Edelfisch" population continued, particularly in the course of the nineties of the last century. One factor responsible for this may also have been erroneous measures of the so-called Concordat Commission which, strange as it may seem, established a closed season from October 1st to November 23rd in analogy with the federal fishing laws enacted in 1888. Thus the "Edelfisch" were not protected during their spawning period, but only after its conclusion'. In 1900 the closed season was sensibly again set from July 25th to September 30th. The result was a rapid increase of stocks, so that later on the season could again be shortened. In addition to this a number of fishermen were authorized to fish at designated spawning grounds, using ground nets with a minimum mesh of 38 mm. The number of authorized fishing places and the type of nets used was, as far as possible, limited. Unfortunately, the spawning products which are thus brought to the surface cannot usually be utilized because the spawners almost invariably lose all their eggs in the course of being raised in the nets from depths, which causes their swimming bladders to bloat, and also because the warm season is unsuitable for the breeding of coregonine fry in artificial breeding plants. The yields achieved in these spawning period catches vary, but they are quite considerable. After the conclusion of the spawning period, fine mesh nets can again be used. The fishing statistics show that approximately two and a half times the number of "Edelfisch" were caught in the "inner" lake than in the "outer" lake.

As far as the catch of "Balchen" is concerned, it is much smaller than the "Edelfisch" catch. The "Balchen" are caught by means of shore drawnets or, occasionally, also with other fishing devices. Even today in the main still with the aid of "firing" (Translator's Note: Local Swiss meaning of this word not clear from text.) As a result of this fishing during the spawning period of the Balchen, great quantities of spawning material which can be used for artificial breeding is obtained, but in the main the older age groups are caught. Probably young Balchen are not recognized as such and are frequently caught together with the "Weissfischchen" in fine mesh nets. Whether the assumption that the introduction of alien Balchen (from Sempach Lake, from Lake Neuchatel -- for the last 7 years, several hundred thousands of fry -- and others) is causing the original Balchen population to die out and be replaced by a more or less floating type which spawns in winter, is correct can hardly be decided at this stage.

In the course of the most recent period of time we have received reports of a considerable increase of winter spawning large coregonines in Lake Lucerne. In 1949-50, for example, there was an unusually large amount of coregonine fry. From the reports it is not quite clear whether only the old "Balchen" which are definitely shoreline spawners, were caught and artificially propagated, or also the new so-called "Blaufelchen" ("Blue coregonines") which have been observed in the region of Stans and Alpnach as well as other parts of the lake, all the way to Brunnen. Some fishermen maintain that the spawning period of the "Edelfisch" has simply moved into autumn, others believe that the restocking with floating coregonines from other lake regions is now beginning to pay off. The development

which will take place in the next few years is awaited with great interest. Lake Lucerne is at the moment subject to some noticeable transitions. We are once more reminded that nature does not stand still but that everything moves, and that in spite of all efforts on our part, we are only capable of creating momentary pictures which may have to be corrected a few years hence. Naturally these events are also fostered by the diligent re-stocking of the lake with foreign fry. In view of this it appears even more important to re-examine the state of affairs carefully from time to time.

Illustrations p.415 German text

Illustration 43 -- "Balchen" from Lake Lucerne caught dead weight approximately 600 g.

Illustration 44 -- "Balchen" from Lake Lucerne "Primigenius type".

Illustration 45 -- "Edelfisch" from Lake Lucerne.

Illustration 45 -- "Weissfischli" -- Albeli from Lake Lucerne. Winter Albeli.

According to the regulations presently in force, fishermen have the following types of net at their disposal: floating nets (33 to 40 mm.) bottom nets for Edelfisch (38 to 40 mm.), for Albeli (25-26 mm.). In addition to that the so-called "land yarn" with various mesh gauges of the "bag" depending on the fish to be caught.

NOMENCLATURE

The coregonines of Lake Lucerne should, according to our principles, be called:

1. "Balchen" = "Blaufelchen" (winter spawning large coregonine) = Coregonus lavaretus L. nat. riusensis, ecotype primigenius.

2. Edelfisch = Coregonus lavaretus L. nat. riusensis,

ecotype pelagicus.

3. "Albeli" or "Little White Fish" = Coregonus lavaretus L. Nat. riusensis, ecotype nanus,

which should really be further differentiated according to whether they are "Winter Albeli" or "Summer Albeli". In view of the fact that these two do not in any way differ morphologically, and also since the possibility cannot be excluded that partial populations which, as a rule, escape the attention of fishermen, also spawn between the two spawning periods, in other words, in autumn, we have decided for the time being to coin no special names to designate the summer and winter spawners. Perhaps populations which constantly inhabit the depths should be designated separately as Coregonus lavaretus L. nat. riusensis, ecotype profundus.

	Circumference	Head Length	Eye Diameter	Caudal Peduncle
Balchen	48-59.5	15 -18	2.5 -4.5	5.25- 9
Edelfisch	46-62.5	14.5-19.0	3 -4.75	5.75-13.25
Albeli	44-56	15.5-22	3.25-5.25	6.25- 9.5

	Pectoral Fin Length	Scale Count	Gill raker teeth
Balchen	10.5-15	77-102	20-31
Edelfisch	11 -16	75-105	31-42
Albeli	11.5-16.5	69- 93	35-42

G. SARNER LAKE

We are considering Sarner Lake as being one of the lakes of the Lower Alpine region. While it is true that its elevation above sea level is only some 40 meters more than that of Lake Lucerne, which has been designated a "lake of the marginal Alpine region", its natural conditions are such as to cause it to be significantly influenced by the lower Alps and their waters. The Lake which has a mean depth of 31.9 meters, a maximum depth of 52.4 meters, has a volume of .244 cubic kilometers. Its area amounts to 7.64 square kilometers. Since the shores of this Lake are flat in many places, it appears to have a certain similarity to bodies of water usually found in locations of intermediate altitude above sea level, and it also produces quite a considerable growth of weeds.

The list of coregonine lakes as compiled by FATIO fails to mention not only Lungern Lake, but also the second of the Obwalden lakes, Sarner Lake. The coregonines of this Lake are also not mentioned in WAGLER's studies nor in the overall compilation in the Manual of Central European Inland Fisheries. Nevertheless, Sarner Lake has over a period of years developed into a coregonine lake giving good yields and promises to become one of our best coregonine lakes.

Today it can be assumed with certainty that Sarner Lake has been the home of coregonines ever since primaeval times. We know of a certain fisherman called

NAPFLIN who fished for coregonines in Sarner Lake around the middle of the nineteenth century. After this the interest shown in net fishing in the Obwalden region appears either to have fallen off or to have concentrated itself on fishing from the shore. In any case, the tradition of fishing for coregonines disappeared with the passage of time thus causing FATIO to overlook the coregonines of Sarner Lake in his studies. This omission on the part of a well-known fish expert caused the inhabitants of the Obwalden region to develop a plan.

In the nineties of the last century Dr. ETTLIN from Sarnen, an enthusiastic nature friend, repeatedly sent coregonines from Sarner Lake to FATIO for investigation. The latter mentions this in short reports and declared that the coregonine of Sarner Lake would have to be considered as belonging to the Balchen group (according to him, Coregonus schinzii heveticus, basic form balleus). On November 18, 1896, FATIO received one more coregonine from Dr. ETTLIN. This specimen had a longer snout, and FATIO designated it as being close to the "Edelfisch" of Lake Lucerne, and he actually identified it by the name Coregonus wartmanni nobilis. Thus, around the turn of the century FATIO assumed that Sarner Lake contained a bottom coregonine and a floating coregonine, but according to his opinion, the coregonine population of the Lake was small. Today we have to ask ourselves whether it could not have been possible that the coregonines even at that time were already quite

plentiful in this Lake, and whether it wasn't lack of knowledge on the part of the fishermen which were responsible for the apparent lack of fish in the Lake.

Around the turn of the century the state of fisheries in Sarner Lake was investigated by Prof. HEUSCHER. As a result of his investigation and also on the initiative of the then Director of the Obwalden Police, Mr. A. KUCHLER, several test catches were conducted during the first years of the century. In 1903 for example two "Rotel" bottom nets with a mesh of 24 and 26 mm respectively were set with the surprising result of no less than 69 "Balchli", having an average weight of only 100 grams, being caught. The Reverend Father JODOK RIGERT, to whom we are indebted for particularly significant data, reports very bountiful catches of Sarner Lake "Balchli", twelve of which always weighed around 1 kilogrammes. Soon after this, spawning fishing was also begun, and the spawning material thus obtained was placed in an artifical breeding installation established by Mr. AUGUSTIN WIRZ, Fisheries Inspector. This systematic introduction of new stock based on locally obtained spawn is responsible for the fact that today the "small coregonine" population of Sarner Lake is unusually numerous. We cannot give any absolutely accurate data concerning the number of juvenile coregonines introduced into the Lake, because for a period of seven years subsequent to 1913 breeding material originating from Sempach Lake coregonines was introduced into Sarner Lake in

exchange for lake trout spawning material which was supplied to the canton of Lucerne. We do, however, know that, for example, in 1916 more than 10,000 Sarner Lake "Balchli" eggs were artificially bred, in 1917 168,000, in 1918 180,000. In subsequent years this breeding of local material increased considerably:

1911/12:	500,000
1913/14:	840,000
1934/35:	1,000,000
1938/39:	1,152,000
1941/42:	1,466,000
1942/43:	1,578,000
1943/44:	2,100,000

Ever since the beginning of this century we also know that Sarner Lake is inhabited by quite a considerable number of small coregonines. In a report made at the time by the Police Directorate of the Cantons Obwalden, mention is made of the fact that two different varieties were being caught, Evidently the two types already differentiated by FATIO. It will be difficult to decide to what extent the development of these "Sarner Lake balchli" are a modification of the autochthonous coregonine form as a result of introductions which took place during the last years of the nineteenth century. It is, however, certain that around the year 1900 the fishermen of the Obwalden region did speak of an "original form of Sarner Lake coregonines".

Thus, even though the coregonine fisheries

of Sarner Lake experienced a considerable boom up to the Second World War, there was no change in the unpleasant fact the "balchli" of Lake Sarner continued to show a very slow rate of growth. Experts assumed that this poor rate of growth was caused by an inter-relationship between the original coregonine of Sarner Lake with the dwarfed "weissfischli" of Lake Alpnach and Lake Lucerne. One thing is certain, and that is that the "balchli" of the Sarner Lake could only be caught with fine mesh nets, and that wider mesh nets which were repeatedly tested were unable to produce catches.

In the course of the last ten years the reputation of the "balchli" of Sarner Lake has spread far and wide. In the trade their role can be compared to that of the "bondelles" of Lake Neuchatel, and they actually show an exceptional similarity in size and growth to the "bondelle". Their average size and weight surpasses that of the "weissfischli" not inconsiderably. In the course of the last few years there have first been isolated and more recently constantly increasing catches of larger coregonines. This is generally thought to be due to introductions of large coregonines, particularly from Sempach Lake. Ever since 1940 there also has been an increasing use of wide mesh nets with ever-increasing success. The fact that a larger tribe of coregonines is in the process of development is clearly evident, and the resulting boom in the fishing industry of Sarner Lake

promises to be of some economic significance.

In our collections and investigation reports we have compiled considerable material concerning the small and large coregonines of Sarner Lake. Since 1938 we have conducted individual, and, in the years 1944 and 1945, systematic series investigations. Thus, we are today in a position to give a situation report about the movement of population among the coregonines of Sarner Lake.

Sarner Lake today contains a mixture of different coregonine types. On the basis of our measurements we are, however, able to give a certain amount of emphasis to two types. Without at this stage wishing to establish any scientific nomenclature, we simply call these two tribes the "Sarner Lake balchli" and the "Sarner Lake large coregonines".

THE SMALL SARNER LAKE COREGONINE ("Sarner Lake Balchli")

Mature fish having a length of approximately 22-26 cm. Almost without exception three years old. Among the 25-26 cm long ones also some four year old specimens, some of whom appear to be in their second spawning period. They are males and females used for the purpose of artificial breeding.

Co-efficient of slimness...in most cases under 50%, Maximum 52.7%

Head length...17-18%, which must be considered as normal in view of the body length

Eye size index...4.4-5.1%

Caudal peduncle...fairly slim

Pectoral fin...large. The largest examples have the largest fins both absolutely and relatively.

Scale count...80-93

Raker tooth count...mostly 38-41

Sooty colouring of fins...very minute in the case of three year old specimens, somewhat more noticeable in four year old ones

The stomach content which almost invariably consisted of lake bottom components with pisidia predominating was particularly worth noting. These fish were caught throughout the year, and, in particular during the winter spawning period by means of narrow mesh ground nets. Floating net fishing methods have only been used in most recent times.

THE LARGER COREGONINES OF SARNER LAKE

It is difficult to decide just how long this type has been present in the Lake. The specimens sent to Dr. FATIO, which we discussed previously, measured around 30 cm. We have in our possession a 32.5 cm long specimen dating from the year 1938, and in 1944-45 we were able to examine more extensive series during the spawning period.

If, after eliminating all six, seven and eight year old fish, we subject the four and five year

old ones to a special study, then we see that the majority of these fish reach a length of 26 to 30 cm. The higher age groups achieve a length of 32 to 40 cm, but when they do they are in their second, third or fourth spawning period. Among the three year olds, which are still immature, there are individuals measuring 20 to 24 cm, which we designate as young "large coregonines". The majority of the coregonines in this size group caught in the Lake reach sexual maturity in their third year, that is to say, they belong to the "small" type. The four and five year old fish, the scales of which show they have already passed through a spawning period, must also be considered separately from the "large coregonines". In fact, we have encountered several specimens, which at the age of four years only achieved a length of 23.9 to 25.5 cm, and at five years one of 26 to 27.5 cm. Thus, while the "balchli" spawn as early as the third year and have only a poor rate of growth in the subsequent years, the "large coregonines" reach a length of 24 cm in their third year without, however, reaching sexual maturity until their fourth year.

When we subject this later spawning group to a vario-statistical investigation then we are able to recognize:

Stature...more compact than the smaller tribe

Co-efficient of slimness...usually considerably more than 50, in isolated instances up to 63%

Eye size index...somewhat smaller, in most cases around 4%, occasionally less than 4%

Pectoral fins... on an average larger than those of the smaller tribe, a fact which can be explained by the higher average age

Gill raker teeth...somewhat less numerous, in most cases 35 and 36, in isolated cases only around 30

It is evident that this type is close to the primigenius of Lake Lucerne and also of Lunger Lake.

On the whole, one tends to gain the impression that -- probably as a result of crossings of "large types" whose growing periods lasts longer and who mature at a later date -- a larger type has begun to consolidate itself from the original small "balchli" of Sarner Lake. This larger type seems to have somewhat fewer gill raker teeth, and other characteristics which separate the "large coregonine" from the "balchli". It is possible that this "Status 1950" based on our present-day knowledge will change again in subsequent years, but as matters lie at present we believe that we are correctly interpreting the events taking place in Sarner Lake by assuming that the era of the small coregonine is gradually drawing to its close, and that the larger tribe will be the victor.

It may be noticed that the weight of the coregonine yield of Sarner Lake has recently increased considerably. In future we shall be able to use the larger mesh net with increasing frequency, and we will thus conserve the immature "large coregonines",

particularly in the floating regions, while we should use narrow mesh ground nets to prevent the "balchli" living closer to the lake bottom from multiplying too fast. By means of artificial breeding, efforts will have to be exerted to favour the "large coregonine" type. This is also the goal pursued by Mr. BRITSCHGI, Master Fisherman, who with his private breeding station must be given a great part of the credit for the management of the Lake.

NOMENCLATURE

The "Sarner Lake balchli": Coregonus lavaretus L. nat. riusensis ecotype pelagicus-nanus.

The "Sarner Lake felchen": Coregonus lavaretus L. nat. riusensis ecotype primigenius.

	Circumference	Head Length	Eye Diameter	Caudel Peduncle
"Sarner Lake felchen"	45.5-63 Mean 63	14-21 Mean 17.5	3.5-5 Mean 4.5	6.5-9.5 Mean 8.0

	Pectoral Fin Length	Scale Count	Gill Raker Count
"Sarner Lake felchen"	11-18.5 Mean 14.5	69-93 Mean 82	29-41 Mean 36

H. ZUGER LAKE

Zuger Lake, which is located 417 m above sea level, is with its maximum depth of 198 m and a mean depth of 84 m, quite a considerable lake. Surface area approaches 38 sq. km, and its volume which amounts to 3.2 cubic km, is almost equal to that of Lake Zurich

which is twice as large. A characteristic feature of this Lake is the small amount of water entering it and, thus, the extended period required for a complete change of water to take place. This circumstance, which makes the Lake particularly sensitive to pollution, also affects its fishing industry.

The coregonines of Zuger Lake have been the subject of ichthyological investigations. In the nineteenth century the fishermen themselves were of the opinion that their Lake was inhabited by one "large" and one "small" coregonine. They called the former "balchen" and the latter "albeli". Opinions, however, differed as to whether the "albeli" represented a particular species, or should be viewed merely as a juvenile form of the "balchen".

FATIO who had several "albeli" sent to Geneva based his species diagnosis on this special investigation and spoke of an "albeli-albock (Coregonnus wartmanni compactus), which he compared to the "blue coregonine" of Lake Constance. Since this fish, however, was more compact than the "blue coregonine" and had a more massive head, and also had certain other characteristics of the "balchen", he established a new species. His own description is fairly indistinct:

> "Corps médiocrement allongé, plutôt épais et assez convex en avant; pédicule caudal moyemment allongé, quoique plutôt étroit...Œil moyen... pectorales moyennes, etc."

The data concerning the gill raker count, which appeared to fluctuate from 35 to 39, and the figures given for the body length of adults and "old" specimens (25 to 33 cm) -- in other words, quite a considerable length for a "small coregonine" are of some interest. The scale count is given as varying from 76 to 86. FATIO's statement concerning his decision to classify the "albeli-albock" with the "wartmanni" type is characteristic. He admits having vaccilated for a long time whether he should include the "albeli" with the "exiguus" type -- for example, with the "albeli" of Lake Lucerne -- or whether he should consider it to be a "large floating coregonine". After he had received a series of larger specimens -- measuring up to 36 cm in length -- he decided to place the fish into the group of the "blue coregonines", but he emphasizes various points of similarity with the "exiguus" type; small, not evenly paired fins, slight pigmentation, number of vertebrae, etc. He also leaves the question of whether or not, as certain fishermen assume, there was a further type of "small coregonine" present in Zuger Lake unanswered. In any case, he is of the opinion that the size of the floating coregonine of Zuger Lake when it first begins spawning frequently is smaller than that of the "blue coregonine", and its Alpine relatives. FATIO gives the spawning period as lasting from September to the middle of October, and he states that the spawning takes place near the centre of the Lake and at depths of 150 to 180 m.

As early as 25 years before FATIO - i.e., around 1870 -- complains about decreases in the number of this coregonine were heard, and the pollution of the Lake and its tributaries made responsible for dwindling populations.

Before publicizing our own observations, we would also like to take issue with FATIO's views concerning the "balchen", the other coregonine form of Zuger Lake.

FATIO places the "Zuger Lake balchen" (Coregonus schinzii helveticus var. zugensis) in the same line as the "balchen" of Lake Thun and Lake Lucerne, as well the "sand coregonine" of Lake Constance. The variety found in Zuger Lake is described as "slim". Its head is designated as more elongated (plutôt allongée). The caudal peduncle is also said to have only slight width, and the number of vertabrae is said to be low, amounting only to 61.

All these characteristics appear to express an approach to the "albeli". Only the gill raker tooth count (19 to 24) is very low -- so low that FATIO even considers a comparison to the "kilch" of Lake Constance. Throughout FATIO's great lack of assurance becomes evident, and even by only reading the relevant chapters the impression is created that the "albeli" and "balchen" are very close to each other. According to FATIO, the spawning period of "balchen" falls within the latter third of November up to December 8th or 10th. "Shallow shore waters" are indicated as the spawning place.

In the subsequent period entirely different data was reported by fishermen on Zuger Lake. The "albeli" was called "whitefish" in 1892 and placed alongside the "small coregonine" of Lake Lucerne. People did not want to hear anything concerning the "albock" proper, but they gave the large coregonines of Zuger Lake the general designation of "Zuger balchen". In 1907 the assertion is even made that there also was a "blue coregonine" in Zuger Lake, and that contemporary fishermen called it "blauler" or "blauling". Dr. HOFER at that time investigated the coregonines of Zuger Lake and emphasized that "blauler" had a steel blue colouring reaching over its back. The scales were reported as being somewhat finer than those of the "balchen", and the gill raker teeth were said to stand closer to each other. The following table concerns information concerning the results of HOFER's investigations:

Blauler:			Balchen:	
	a)	b)	a)	b)
Length.....	33.3	35.3	44.8	46
Weight.....	300	330	660	810
Head length.....	5.7 = 17.1% of the length	5.7 = 16.13% of the length	7.4 = 16.5% of the length	7.5 = 16.37% of the length
Eye diameter....	12.5 mm = 3.75% of the length	12 mm = 3.39% of the length	14 mm = 3.12% of the length	15 mm = 3.25% of the length
Lateral line....	$85^{9}/_{8}$	$83^{9}/_{7}$	$91^{9}/_{7}$	$97^{10}/_{8}$
Height.....	6.8	6.5	8.4	10.2
Tail fin.....	Upper point shorter than lower point in most cases	Ditto	Both tail fin points equal in length	Ditto
Egg size.....	100,000 per litre	Ditto	60,000 per litre	Ditto
Spawning location...	In all depth zones of the Lake	Ditto	Close to the shore-lines	Ditto
Spawning season.	Second week in September to middle of October	Ditto	Last third of November to first third of December	Ditto

Insofar as one can make any conclusion based on investigations carried on on the four specimens, it appears that the main difference existed in the size of the scales. In addition to this, the "blauler" is said to have uneven tail fin flaps (heterozerk), while the "balchen" is said to be normal in this respect.

On the basis of his own investigations conducted at the site, E. WAGLER is lead to maintain that he has seen nothing but "floating coregonines". He has evidently, however, neglected to determine the gill raker tooth count. Zuger Lake is not included in his tables.

On instructions of the COMMISSION OF THE FISHERIES AGREEMENT FOR ZUGER LAKE, I conducted an investigation of fisheries conditions in Zuger Lake in the course of which I took advantage of this opportunity to conduct extensive studies dealing with the coregonine populations. A study published in 1939 in the "Schweizerischen Fischereizeitung" ("Swiss Fisheries Journal") initially deals with the most basic aspects. An expert opinion compiled by me as chairman of a four-member commission of experts and addressed to the cantonal governments concerned discusses the details. The following explanations and data are based on this material, as well as on the collections of material left at the Aarau Museum.

Today Zuger Lake contains but one form of coregonine which we will designate as "Zuger balchen". This is a "large coregonine" of the "Palee" or "Fera" type but with a very considerable tendency towards variation of

the various physical characteristics. It appears that a dwarfed modification has also taken place some time in the past. This sub-species, the very same which was called "albeli", has today become practically extinct. Throughout the whole of the duration of my investigations which lasted several years, I obtained only three "albeli". In addition to this, I was also able to investigate old material found in Swiss museums.

THE "ZUGER LAKE ALBELI"

The part it played appears to be very similar to that of the "bondelle" in Lake Neuchatel: It was a dwarfed sub-species adapted to living in the free water regions and had greater depths, and it had characteristics indicative of the more one-sided living habits predominating in the "floating regions". This was particularly indicated by its somewhat more numerous number of gill raker teeth. First of all, we want to acquaint our reader with our material.

OLD MUSEUM SPECIMENS

Geneva: Designation Albeli-Albock, Doregonus wartmanni compactus FATIO, or Coregonus macrophthalmus var. zugensis nusslin.

No. 1: 33 cm in length, 6 years old, with the following age characteristics: Co-effecient of slimness 59.4, head length index 18.2%, eye diameter 3.7%, pectoral fin length 15.1%, scale count 84, gill raker tooth count, more than 30. It could not be accurately recounted. Two dried specimens exhibited in the Geneva

Museum show 38 and 39 gill raker teeth respectively.)

A very similar specimen is found in the Basle Museum. It is a somewhat slimmer male 5-year old. In addition to this, a 4-year old male belonging to the same type. These two measure 31.5 and 28 cm respectively.

Much smaller and having much more of the appearance of floating coregonines is a 3-year old specimen measuring 23.5 cm in length which is found in the Geneva Museum: Co-efficient of slimness 52.6%, eye size 4.4%, scale count 78 -- while an albeli caught on December 5, 1890, and contained in collections of the Aarau Museum is a 24.3 cm long 3-year old female. This specimen also has large eyes (eye diameter 4.7% of the body length). Co-efficient of slimness 58.

FRESH MATERIAL

Insofar as fresh material is concerned, I was able to examine 2 females and 1 male in 1937, and I am reproducing the measurements here in view of the present-day scarcity of this type of material:

	Length	Weight	Co-efficient of slimness	Head length	Eye size	Caudal Peduncle length
No. 17 ♀	28.2	300	49.6%	19 %	4.3%	7.45%
No. 18 ♀	24.4	140	49.6%	18.9%	4.5%	7 %
No. 19 ♂	32.8	350	50.3%	18.6%	3.7%	7.2 %

	Pectoral fin length	Scale Count	Gill Raker teeth	Age
No. 17 ♀	11.4%	78	30	4 years
No. 18 ♀	13.1%	76	38	5 years
No. 19 ♂	13.3%	74	29	4 years

Numbers 17 and 19 showed a strong spawning epidermis (end of November). No. 19 certainly is not a typical albeli (the eye size, gill rakers, relative size). Not only these but also many "balchen" which will be discussed subsequently convinced me that the albeli type is connected to the balchen type by certain connecting links, and that a division implying the creation of a special species is by no means justified. No. 18 is a strongly dwarfed old specimen, No. 19 a young specimen with hardly any signs of dwarfing.

According to FATIO, the former albeli spawned at great depths at the centre of the Lake. As a result of increasing pollution of Zuger Lake, the spawning grounds have evidently become part of the "hydrogen sulphide zone", which is poor on oxygen and can no longer be used. This has caused the albeli to die out as fishermen appear to think, or whether corresponding changes in its living habits and adaption to a new habitat and to new spawning conditions have resulted in renewing its similarity to the "balchen" type is a difficult question to decide. Of course, here again the possibility of cross-breeding with alien coregonine material must be taken into consideration as a possible cause for changes. In any case, by now the number of typical "dwarfed balchen" or "albeli" has become very small.

"THE ZUGER LAKE BALCHEN"

FATIO has called this principal fish of Zuger Lake "Coregonus schinzii helveticus var. zugensis".

The main features of the older museum specimens show such a large measure of agreement with the extensive material I, personally, subjected to direct investigation, and it is, therefore, not necessary to deal with them separately. It is evident that the museums were concerned in obtaining "exhibition specimens", and in view of this their collections contain old fish (Basle in 1906, 7 and 8-year old, 45 cm long specimens).

My own material includes "balchen" having lengths from 28 to over 50 cm and all age groups from 3 weeks to 8 years.

It appears that fishermen also carry out a certain differentiation when sorting their balchen material, as, for example, they separate "blauler" ("blue ones") from the dark fish, and they also speak of "floating balchen" and "bottom balchen". On one occasion I was shown a "brown balchen" which was said to belong to the "old sort", while, in the opinion of a fishermen who gave it to me, the "blue ones" corresponded to the "blue coregonines" of Lake Constance, a tribe which, in fact, on repeated occasions supplied breeding material for Zuger Lake. We have invariably investigated such special cases with particular care, but we became convinced that it is impossible to isolate individual types from the whole considerably varied population and to describe these types separately. In particular it was established that the gill raker tooth apparatus of the "blues ones" by no means corresponds to that of the "blue coregonines" of

Lake Constance. The tooth count, however, fits well within the variation range found in the "balchen", and through various publications in the course of several decades we had the opportunity to become acquainted with the "blue blauen" of Zuger Lake. We have to repeat our observation that their so-called "basic colouring" of coregonines is to a great extent governed by environmental factors and is, therefore, quite unsuitable for the purpose of establishing differential diagnosis.

Having considered all factors, we come to the conclusion that the present coregonine population of Zuger Lake cannot possibly be divided into species or sub-species, not even into races and tribes in view of the great variability of all possible characteristics. The only thing that could perhaps be stated is that on an average the "balchen" living on the Lake bottom and closer to the shore have a somewhat shorter cordal peduncle than those caught in the free Plankton regions.

As far as the nutrition and reproduction of the balchen of Zuger Lake is concerned, it can be stated that during the warm season they principally feed on plankton. One gains the impression that coregonines caught in so-called floating nets in every way behave like "floating coregonines". In the coregonines caught close to the shore plankton crustations are mixed with litoral elements, in particular with insect larvae. Even vegetable particles are occasionally found. Since I had to rely on spot checks, I cannot claim that my data is in any way complete.

Reproduction takes place around the end of the year. It usually takes place close to the shore where the water is not very deep or even shallow. In earlier times "balchen" are said to have spawned in deeper water as well. Probably the increasing pollution of the depths of the Lake is responsible for this change. For decades the "balchen" of Zuger Lake has been the subject of careful management in breeding ponds, and the ancient fish-breeding station at Zug in which the first "Zuger glasses" were used is world renown. Unfortunately the rapidly increasing pollution of the Lake which has a relatively great depth and small surface area, and, in addition to this a very slow rate of water replacement makes all efforts of the fish-breeders problematical. Very considerable damage has been caused by the so-called "Burgundy Blood Algae". The coregonine population is occasionally also subject to certain diseases, particularly the Triaenophorus crassus and Henneguy zschokkei. The first of these diseases forced those responsible for the management of the Lake to decimate the population by means of intensive hause yarn fishing, which brough about a considerable improvement.

NOMENCLATURE

Zuger Lake balchen: Coregonus lavaretus nat. riusensis ecotype primigenius.

At present a subdivision is still impossible since the ecotype has not consolidated themselves sufficiently.

Zuger Lake albeli (extinct): Coregonus lavaretus nat. riusensis, ecotype primigenius nanus.

	Circumference	Head Length	Eye Diameter	Caudal Peduncle
Balchen	46.5-57.5	15.5-19	3.25-5.75	6.25-9.75
Albeli	49.5-52.5	18 -20	3.5 -4.75	7 -8.75

	Pectoral Fin Length	Scale Count	Gill Raker Teeth
Balchen	11 -17.5	76-88	21-36
Albeli	11.5-15.5	73-84	24-38

K. AEGARI LAKE

Lakes of the Alpine level like Aegari Lake which lies 728 m above sea level are naturally subject to mountainous conditions. They freeze up every year, and the ice cover is often maintained into late spring. The surface area of Aegari Lake is almost as great as that of Sarner Lake (7.24 sq. km), but as a result of its great depth (maximum 82.7, mean 49.3 m) it has a considerable volume amounting to .357 cubic km. It is certain that there are no natural occurrences of coregonines in Aegari Lake. The fishes of this Lake, particularly the so-called "Rötel" have been known and valued for a long time, since there is no doubt that had there been any coregonines in the Lake, they would have been caught in the course of the quite intensive fishing operations taking place there.

According to SURBECK (1917) attempts to introduce them were made as early as in the eighties of

the last century. The breeding material came from the famous Zug fishing station, and the mother fish were Zuger Lake balchen. Later on, coregonine eggs originating from Pfäffike were also used. First, no success whatever could be noticed, and it was assumed that the very abundant "Rötel" had destroyed the young coregonines each time.

The first coregonine from Aegari Lake was caught on November 24, 1916, by Mr. MERZ, a fisherman at Cirhals. It had been caught by chance in a "Rötel" net and was subsequently preserved in alcohol. SURBECK had an opportunity to investigate it in January, 1917: It was a 2-year old specimen, measuring 18 cm in length and having 22 gill raker teeth. It was considered to be a descendent of the Zuger Lake balchen.

Since that time the coregonine stock of Aegeri Lake developed quite favourably so that today even though this Lake is located at a fairly great elevation, they play a considerable part in the fishing industry. We are using the following figures obtained by us in 1939 and 1944 in order to characterize present-day coregonine of Aegari Lake: Material obtained from a 40 mm floating type net, 300 to 400 m from the shore at a depth of 12 to 15 m. Number of investigated specimens: 23 - 11 male and 12 female. Age (investigated in August) from 1½ to 4½ years. Size ranged from 18.1 to 36 cm and weight from 35 to 415 grams.

In their growth the balchen of Aegeri Lake correspond to the balchen of Zuger Lake. Their scale size (scale count 72 to 104, mean 83.6) and the number of their gill raker teeth (21-30) caused them to be classed with the Primigenius group, which also includes the Zuger Lake balchen. Five of the specimens investigated, i.e., a high percentage, showed the well-known heterozerke tail fin which is so frequently found in Zuger Lake. The relatively high elevation of the Lake did not appear to affect the growth: 3½-year old specimens reached the 30 cm limit. It appears that maturity in most cases takes place in the fourth year of life. As is the rule for fish of the "large coregonine" type, the gonad development is good, several examples were extraordinarily adipose.

Since according to FATIO, the former Zuger Lake balchen which he called Coregonus schinzii helveticus var. zugensis had 19 to 24 gill raker teeth, and since SURBECK also gives figures close to the lower limit of our range, it can be concluded that the coregonines of Aegari Lake in the course of the approximately fifty years of their stay in this Lake have slightly increased the number of their gill raker teeth. In other words, they are in the process to differentiate themselves in the direction of the "floating coregonine". Nevertheless great care must be taken when making such statements.

The exact distribution covering all the individuals comprising our material is evident from the

following table:

Gill Raker Teeth	21	22	23	24	25	26	27	28	29	30	total
No. of Individuals	1	1	3	2	5	4	3	-	-	2	21

In 1917 SURBECK expressed a wish to the effect that it would be desirable in future years when the coregonine population of Aegari Lake has become consolidated and strengthened to examine whether the gill raker tooth apparatus remained similar to the original species, or whether the new conditions of life caused it to begin changing in a manner similar to that reported by THIENEMANN in the instance of the well-known coregonine of Laacher Lake. On the basis of our findings to date, we can give the following reply to this question: The number of gill raker teeth of the coregonine of Aegari Lake is greater than that originally found on the "balchen" of Zuger Lake. At the time it supplied the stocking material for Aegari Lake. In the meantime conditions in Zuger Lake have, however, also changed (compared with the chapter dealing with Zuger Lake).

In the course of the last few decades the coregonines of Aegari Lake have developed into the principal fish of the area. A diligently conducted programme of coregonine breeding evidently represents a considerable contribution towards increasing the yield of this Lake. In most recent times even recreational fishermen enjoy an ever-increasing interest for the Aegari Lake coregonine. Ever since it was shown that it can be easily caught by means of so-called jerk angling. A problem which has recently arisen is the decrease in the "Rötel" population which goes hand-in-

hand with the increase in the number of coregonines. There are certain indications that a similar process is also taking place in Zuger Lake and in Lake Lugano. It has, however, not been established whether competition for food supply or direct persecution and displacement caused this antagonism. Probably there is a further third motive which influences the population fluctuations. Whenever density of a swarm increases, it brings about an increase in the percentage of sick members of the swarm. In Aegeri Lake the boils caused by Henneguya zschokkei were particularly noticeable, while the triaenophorus-crassus plague prevalent in Zuger Lake has as yet not been noticed. When considering fluctuations in yield, the effect of plagues must certainly be taken into account.

NOMENCLATURE

The coregonine of Aegeri Lake must bear the name of the "large coregonine" of Zuger Lake and consequently it must be called: Coregonus lavaretus L. nat. riusensis, ecotype primigenius. It thus enters the lines of the "balchen" of Lake Lucerne, with whom it actually shares a number of significant characteristics.

AEGERI LAKE

Circumference	Head Length	Eye Diameter	Caudal Peduncle
42.5, Mean 49.27	14.5, Mean 17.42	3.5-5, Mean 3.92	6.5-11, Mean 7.97

Pectoral Fin Length	Scale Count	Gill Raker Teeth
10.5-15, Mean 12.46	72-104, Mean 83.6	21-30, Mean 25.7

L. LOWERZER LAKE

Lowerzer Lake is located 451 m above sea level. It is embedded between Rigi and the Goldau avalanche deposits. Surface area measures 3.09 sq. km and its maximum depth is 13.2 m. Its mean depth amounts to 7 m. The Lake obtains little sunshine and freezes up rapidly in winter. It is surrounded by a belt of bulrushes and in the past it was mainly considered to be a pike lake. Its tributaries are mountain streams giving an uneven water supply. The Lake, the contents of which is calculated to amount to .022 cubic km, shows strong silting tendencies.

Tiny Lowerzer Lake has (today) not yet figured among the coregonine lakes of Switzerland. At least in the literature available to me I found no reference to the occurrence of coregonines in this body of water. Hearsay (evidence), however, led me to believe that in spite of the slight depth of the Lake, it may well also contain coregonines. I was actually also able to learn from interview eye witnesses who stated that occasionally small coregonines (did land up) in their nets and, finally, through the intermediary services of Mr. OTT, a fisherman of Lowerz, I was able to examine several specimens which showed various interesting peculiarities. In spite of all our efforts, we were unable to obtain any accurate information concerning the origin of the coregonines in Lowerzer Lake. Even the fisheries supervisors of the region were unable to give us information. As a result, we are

unable to say whether we are dealing with an ancient original or a newly introduced population. All sorts of speculations were made, but for decades past no real fishing operation had, in fact, taken place. In 1944 Mr. ITT reported encountering small, silvery fish unknown to him and which perhaps may have been coregonines. In March, 1945, he then sent a first specimen which had very evident characteristics of a high degree of dwarfing, and in the autumn of that year during the spawning period, which appears to take place in November, it was even possible to catch a whole dozen of Lowerzer Lake coregonines which on November 22nd, 1945, were forwarded for investigation.

In order to determine the nature and origin of this coregonine it may well be best first to refer to the gill raker tooth apparatus (see table). The "Weissfischchen" ("little white fish") (albeli) of Lake Lucerne, which in size correspond quite well to the coregonines of Lowerzer Lake, show an entirely different gill raker tooth count. There are also no direct ties linking the Lowerzer Lake coregonines to the "Edelfischen" of Lake Lucerne. The mean values and the variation range of the gill raker tooth count of the Lowerzer Lake coregonines, on the other hand, correspond well to those of the Zuger Lake balchen. The balchen of Lake Lucerne could also be used for comparative purposes.

The other characteristics of the Lowerzer Lake coregonine, which is quite clearly a "small coregonine", all bear testimony to a dwarfing process: Large head,

large eyes, relatively slim body, even in the case of sexually mature specimens. In individual cases the pectoral fin was remarkably large. One fairly old specimen caught in March had unusually long fins throughout, while those caught in autumn showed no such considerable deviations from the norm. A significant feature of these fish is the fact that even at 5 to 7 years of age their weight approaches only 100 g. In this connection it is worth noting that the largest specimens are by no means the oldest. Accordingly, it must be assumed that the degree of dwarfing in Lowerzer Lake is subject to considerable fluctuations. The fertility judged from the weight of the gonads in relation to the body weight is relatively great. This is generally the case with dwarfed forms.

In summarizing, it can be said that at the present a dwarfed form of a bottom coregonine belonging to the Féra type is inhabiting Lowerzer Lake, and that in several respects the dwarfing characteristics correspond to those of "small coregonines" which have undergone a differentiation process from the so-called floating forms. In other words, this is either a parallel case or a convergency phenomenon!

NOMENCLATURE

"Lowerzer Lake felchi": Coregonus lavaretus L. nat. riusensis, ecotype primigenius nanus.

Lowerzer Lake Coregonine (5 - 7 year old)

Lengths	Weights	Circumference	Head Length	Eye Diameter
21.3-25.1	80-115 g	48.2-55.5 Mean 50.1	17.3-29 Mean 18.3	4.5-5.25 Mean 4.9

Caudal Peduncle	Pectoral Fin Length	Scale Count	Gill Raker Teeth
7.5-9.2 Mean 8.5	13.5-16, Mean 14.8	83-93, Mean 87	22-28 Mean 25.3

ECONOMIC SIGNIFICANCE

No real economic significance can be ascribed to the dwarf coregonine of Lowerzer Lake. It is doubtful whether this Lake is suitable for the introduction of coregonines. For the time being its pike and perch stocks are too great to begin any large-scale experimental introduction of coregonine stock.

M. HALLWIL LAKE AND BALDEGG LAKE

The following hydrographic data will help initially to characterize these two typical Swiss midland Lakes:

	Elevation above sea level	Area	Maximum Depth	Mean Depth
Hallwil Lake	452 m	10.29 km^2	48 m	20.6 m
Baldegg Lake	466 m	5.23 km^2	66.4 m	34.0 m

Both Lakes were originally surrounded by a well-developed belt of bulrushes, a greater part of which is still well preserved. The tributaries are quite meagre in relation to the volume of the Lake, and, as a result, the rate of

water replenishment is low. The volume of Hallwil Lake amounts to .215 cubic km, that of Baldegg Lake to .178 cubic km. As a result of the relatively dense population of the valley in which the Lakes are located, and, last but not least, the result of the well-developed industry (Hochdorf, Beinwil, Birrwil), the waters of the Lakes have become polluted to such an extent that the so-called Burgundy Blood algae is constantly spreading and causing a total lack of oxygen in the depths of both Lakes. This has caused the coregonine population to decrease sharply in the course of the last few decades. In the thirties the "Hallwil Lake ballen" had almost become extinct, and the Baldegg Lake ballen a great rarity.

As early as 1882, NÜSSLIN on the basis of several specimens he examined, declared the Hallwil Lake balchen and the Baldegg Lake Balchen to belong to a specific species. He was also followed by FATIO, who described the fish under the name Coregonus annectus (Corégone adjoint, or "mock ballen"). Initially, he had wanted to include them with the coregonines of Lake Murten, but subsequently changed his opinion. Upon examining the differential diagnosis, it is evident that the only significant characteristic given by FATIO is the relatively great number of gill raker teeth (33 -38). Other than that, the fish is more reminiscent of the "balchen" type and it also spawns in the shallow waters close to shore. In this respect, it is noteworthy that FATIO quotes the assertion of a fisherman to the effect that in the past the ballen spawned at

greater depths and had only become shoreline spawners in recent times. FATIO believes that the Hallwil Lake ballen is particularly closely related to the "Rheinlanke" of Traun Lake. According to FATIO, the coregonines of Lake Hallstadt and of Wolfgang and Atter Lakes are also supposed to be closely related to the Hallwil Lake ballen. Today we can do hardly anything with all these efforts towards synonymizing the various types, because the descriptions of contemporary authors in most cases refer to a few isolated specimens, and since no more accurate measurements are available.

On the basis of our own material, we have to state that the variation range of present-day Hallwil Lake ballen is much greater than that given by FATIO. The gill raker tooth counts found by us varied all the way from 23 to 39. The average was 32, in other words below the minimum count given by FATIO. Thus, the only obvious characteristic of the "mock ballen", the relatively great number of gill raker teeth, could not be confirmed by our investigations. Either the Hallwil Lake ballen have undergone a change in the meantime, or the material investigated by FATIO was not sufficiently extensive to allow him to grasp the actual variability limits and to base his calculation of a mean value on reliable figures.

We have taken the effort of comparing the old specimens dating back to FATIO's time and still found in museums, and in the process we were able to determine and here, too, the number of gill raker teeth was lower than

was to be expected on the basis of FATIO's data. Thus, there is no longer any reason to consider the Hallwil Lake ballen as occupying a special position from the species point of view. In all their other features the Hallwil ballen and the Baldegg Lake ballen appear to be intermediary forms between the typical bottom coregonine and the pronounced floating coregonines. The fact that their scale count is relatively high, in other words that their scales are smaller, can be emphasized here because it indicates a closer relationship to the coregonines of western Switzerland in contrast to the "Gangfisch" ("wandering fish"), to which the Hallwil Lake ballen evidently has no direct relationship. All in all the Hallwil Lake ballen appears to be on the same level as the so-called bottom coregonines. It is one of the Primigenius types.

As far as size relationships are concerned, it has been well-known from the earliest days that Baldegg Lake was inhabited by larger "balchen" than Hallwil Lake. Around the turn of the century a correspondent of the SWISS FISHERIES JOURNAL reported that the Hallwil Lake ballen weighed from 150 to 200 g and were 23 to 29 cm long, while the Baldegg Lake balchen did achieve a weight of 250 to 400 g, and a length of 29 to 32 cm. A few years later Mr. LEUTWILER, a fisherman, according to the Fisheries Journal, stated that in both Lakes the fish tended to become fewer in numbers and larger in size. Our present-day material only rarely contains smaller specimens among the

sexually mature fish.

A series of 25 spawning fish from Beinwil on the Lake, subjected to investigation in 1945, resulted in the following weights and measurements:

Body Length.....	Maximum	41.2 cm
	Minimum	27.6 cm
	Mean	31.3 cm
Weight.....	Maximum	660 g
	Minimum	170 g
	Mean	297 g

One specimen caught in May, 1944, measured no less than 51 cm in length and weighed 830 g. This fish, which is preserved in the collections of the Museum for Natural and Local History at Aarau, is unusually slim in shape. The fish in question is a senile specimen, which was found starved to death (Illustration 49). Illustration 49 on page 436 of the German text: Top: Lake Constance: Largest sand coregonine investigated by us, 60 cm long, 2.1 kg, 10 years old, 1949. Bottom: Hallwil Lake: Largest ballen caught, 51 cm long, 830 g, 10 years old, 1944.

The Hallwil ballen, which are approaching extinction, in the course of the last phase of their development generally show a considerable rate of growth. In the meantime, coregonines from other localities have been introduced in the Lake, and will tend to obscure the picture somewhat.

In this connection, it should perhaps also be noted that towards the end of the last century the ballen, both in Hallwil, as well as in Baldegg Lake, was considered the most significant fish from an economic point of view, and that with the development of artificial breeding its numbers were greatly multiplied to the degree where inhabitants of lakeside communities stated that the fish populations have at least doubled in size. Every single year several millions of young fry were planted in the Lake. The main fishing season originally coincided with the spawning season, but, subsequently, around the turn of the century, it was extended to cover the whole year. The enormous "ballen" feasts in the villages along the Lake valley are still vivid in the memory of the people. They also attracted many foreign tourists. In approximately 1908 the decrease became noticeable, and in the subsequent years complaints mounted. Occasional years of failure were relieved by improved catches, but gradually the stocks were seriously reduced. As early as 1908 there were half as many coregonines in Baldegg Lake as there had been a few years previously. Increasing production of new stock and the thinning out of the constantly and threateningly increasing perch population again brought about certain temporary improvements, but their irresistible downward development continued. The main reason for this appears to be the increasing eutrophiction of both Lakes. The industries of Hochdorf are assigned the primary blame for the deterioration of conditions. In any case, a very strongly increased vegetation of Burgundy Blood algae

(Oscillatoria rubescens) is one of the original contributory causes. Whether it will be possible to restore the two Lakes as coregonine lakes by improving the drainage conditions of the shore communities and by introducing alien breeding stock (especially from Sempach Lake) remains to be seen in the future.

Perhaps the very considerable increase in the number of "ballen" caught in Hallwil Lake in 1948 can be interpreted as a hopeful sign. The eggs used for rejuvenation in the main originated from Lake Bienne. The "large coregonine" race in this Lake belongs to the Primigenius group, and it was also quite closely related to the old Hallwil "ballen". Today it would probably be difficult to tell the old from the new type. It is possible that the old coregonine of Hallwil Lake did have a tendency towards dwarfing. In this connection, we are reminded of the "balchli" of Sarner Lake. The tribe now flourishing shows a normal growth in every respect. The fish also has a fine reputation among the population of the Aar region for its good taste. At present it is practically only caught in the course of commercial fishing operations, and, particularly during the spawning period, it is caught for breeding purposes. Several fish-breeding stations use its fry frequently with considerable success.

NOMENCLATURE

Hallwil and Baldegg ballen: Coregonus lavaretus L. Nat. intermedia, ecotype primigenius.

Circumference	Head Length	Eye Diameter	Caudal Peduncle
45.5-59.5	11.6-21	3.0-4.25	4.0-9.5

Pectoral Fin Length	Scale Count	Gill Raker Teeth
9-16.5	76-94	23-39
16.2*)	83*)	43*)

*)Baldegg Lake ballen according to published data

N. SEMPACH LAKE

Sempach Lake is located 507 m above sea level. It has an area of 14.38 sq. km, a volume of .662 cubic km. Its maximum depth is 86.7 m, its mean depth 46 m. In its overall characteristics it can be compared to Hallwil Lake (see page 434 of the German text).

Its coregonines have become famous, particularly as a result of the extremely accurate data concerning the yield of this Lake recorded in documents which cover several centuries and which show that in earlier days a very remarkable significance was ascribed to the coregonine fisheries of this Lake. In this connection, we would like to refer to the "accounts of the Sempach Lake Office concerning the balchen catches in Sempach Lake", variously reproduced (see for example HEUSCHER, Uber die Fischerei in der Schweiz/ concerning the fisheries in Switzerland/ Fisheries Journal, 5, 144 /1897/, as well as VON LIEBENAU, Geschichte der Fischerei im Kanton Luzern/ "History of Fisheries in Lucerne Kanton/). These accounts cover a period from 1418 to 1795 almost without interruption. Twenty-three of the years recorded show catches of more than 500,000 fish per year. In 1600, 894,000 fish were

caught not counting those not reported. Figures of over 100,000 appear in no less than 56 years. It is, thus, evident that at that time the yields were very bountiful, but the fish were almost invariably very small. On the basis of the original reports, I became convinced that even at that time there was some discussion about the existence of more than one tribe of coregonines in Sempach Lake. Unfortunately, we, however, lack more accurate data concerning the differences observed. The artificial lowering of the Lake is considered to be the main reason for the decreasing yield in the 19th century, for it resulted not only in the loss of suitable pastures, but also of the spawning grounds of the fish.

To the contemporary coregonine researcher, this Lake has very little of interest left to offer. Its coregonines must in the main be considered to be the offspring of imported coregonines. It is doubtful whether anything at all of the blood of the old original Sempach coregonine remains. After a period of almost complete regression of the Sempach coregonines, the coregonine economy of the Lake has begun to flourish anew as a result of the initiative of Mr. HOFER, a professional fisherman of Oberkirch. It appears that the new Sempach Lake coregonine can primarily be deduced from the "balchen" of Lake Lucerne, but lately fry from all conceivable lakes has been used so that at present we are faced with a manifold mixture of coregonine which does not offer us much that is useful for our systematic discussions.

We have nevertheless investigated several series and have also sought out the older specimens found in Swiss museums in order to be able to compile certain data concerning the coregonines of Sempach Lake.

FATIO designated the Sempach coregonine with the name Coregonus suidteri, and he emphasizes that his investigations were based on a few specimens placed at his disposal by Dr. SUIDTER during the eighties of the last century. He states that even at that time a considerable decrease in the coregonine stocks was noted, and that simultaneously with this decrease the average weight of the fish increased considerably. In previous centuries the Sempach Lake balchen weighed only some 125 g each, while in the eighties of the last century weights ranging from 375 to 750 g were determined. FATIO raised the question whether the original small coregonine of the Lake should not have been considered a special species which was subsequently displaced by a second previously rare large species. In any case, FATIO himself was unable to clarify the question of the actual character of the old Sempach coregonines. The characteristics of the specimens described by him were the fact that they were supposed to combine the "typical" features of the sandfelchen ("sand coregonine") with those of the "floating coregonine". Consequently, he called the Sempach coregonine, as it appeared to him at the time, "Species composita". The outlines of the body and the shape of the head reminded him of the "balchen" ("sandfelchen", "sand coregonine"). The great number of

gill raker teeth, on the other hand, indicated a closer relationship to the "floating coregonine".

As early as during the years 1895 to 1902 and increasingly from 1911 onwards, considerable quantities of balchen fry from Lake Lucerne were introduced into Sempach Lake. In 1920, SURBECK investigated the coregonines of Sempach Lake with particular regard to any changes which may have been caused by the introduction of Lake Lucerne fry during the previous years. From his study we see that around 1918 the "Sempach balchen" was something between the "balchen" of Lake Lucerne and the Coregonus suidteri described by FATIO. This is particularly obvious when we compare the gill raker tooth counts of the three types.

	Lake Lucerne Balchen	Coregonus suidteri	"New" Sempach Balchen
1st Gill Raker Arch	23-28	38-42	30-36
4th Gill Raker Arch	21-22	24-28	25-28

As early as 1895, HOFER had also established that the great number of gill raker teeth described by FATIO no longer applied. In 1893 HEUSCHER investigated three fish caught during the spawning season. They already showed a greater "similarity to balchen" than FATIO's types. Since by the eighties of the last century fry from Lake Lucerne balchen, Maranes and whitefish had already been introduced to Sempach Lake, it is entirely possible that even at that time a modification of the type as a result of cross breeding had begun to take place. I also, unfortunately do not know how many specimens FATIO actually had at his disposal for his investigations, and it is entirely possible

that by chance he obtained representatives of a tribe in Sempach Lake which happened to have more features of the "floating coregonine type". Thus, the whole state of affairs in Sempach Lake is so confused that even HOFER as early as in 1895 expressed the opinion that "it gives one the willies". In this connection, we would also like to quote SURBECK: "FATIO's systematics no longer suffice as an instrument. A thorough revision of the Swiss coregonine and coregonine systematics as a whole becomes a never more pressing necessity, and whenever possible the whole system will have to be founded on a different basis". SURBECK, in this connection, points out the great variability, the flexibility or plasticity of our coregonines.

In view of this state of affairs, we must in this book of revision limit ourselves to the publication of our own results obtained in the course of the last few years, and for the rest we must leave the question of the "species", to which the Sempach balchen should belong, in abeyance for the present.

On August 11th, 1944, Mr. GOTTFRIED HOFER, a fisherman, sent us 12 Sempach balchen for investigation. They ranged in years from 3 to 6 years and had the following dimensions and weights:

Body length.....	Maximum	42.2 cm
	Minimum	29.9 cm
	Mean	35.1 cm
Weight.....	Maximum	600 g
	Minimum	230 g
	Mean	397 g

Gill raker teeth.....Maximum 38
Minimum 28
Mean 30.2

Scale count.....Maximum 92
Minimum 78
Mean 86

In addition to this, we were able to measure specimens from the years 1892, 1910, 1937 and 1939. The measurements of these further specimens all lie within the above limits. In the Basle Museum there are two further female Sempach balchen purchased from Mr. M. DIEBOLD, a taxidermist at Aarau, around 1910. They measure 44 and 45.5 cm respectively. The 2 fit into the variation limits given above. The fish in question are old specimens (7 and 8 years old).

In summarising, we can consequently state:

1. That we know practically nothing concerning the nature the old, small "balchen" of Sempach Lake, hundreds of thousands of which were caught each year during past centuries.

2. That we are not sufficiently accurately orientated concerning the nature of the Coregonus suidteri to be able to maintain that the Coregonus suidteri described by FATIC in the eighties of the last century on the basis of a few specimens was the only or even the predominant coregonine type of Lake Sempach at that time.

3. That since FATIO, new observations repeatedly indicate that the present coregonine of Sempach Lake is quite close to the "balchen", even though its gill raker

teeth are somewhat more numerous than those of a typical "sand coregonine" of Lake Lucerne.

4. That in most recent times coregonines from various other lakes of Switzerland have been introduced into Sempach Lake so that the present-day fish must, in any case, be considered the "mixtum compositum" on the basis of which no conclusions concerning original conditions can be made, particularly not since in the years immediately following the turn of the century the coregonine population of Sempach Lake decreased very sharply, so that traces of their blood can hardly be reflected in the present-day population.

Illustration 51: Sempach Lake Balchen, Milchner, 6 year old, 40.2 cm, 600 g.

NOMENCLATURE

Sempach Lake balchen (as far as there are still specimens present, and as far as determined on the basis of earlier publications and specimens exhibited in museums): Coregonus lavaretus L. nat. intermedia, ecotype primigenius.

Thus, the coregonine of Sempach Lake has been given the same name as the coregonines of the neighbouring bodies of water (Hallwil and Baldegg Lake). To us this appears entirely justified since on the basis of earlier descriptions, as well as on the basis of our own investigations, we have been unable to determine any significant differences.

Sempach Lake Palchen

Circumference	Head Length	Eye Diameter	Caudal Peduncle
47.5-60 Mean 151.2	15.5-18.5 Mean 17.1	2.75-4.0 Mean 3.8	7-10.75 Mean 8.4

Pectoral Fin Length	Scale Count	Gill Raker Teeth
11.5-14.0 Mean 12.6	78-92 Mean 82.1	26-38 Mean 33.5

O. LAKE ZURICH

Elevation above sea level 409 m; area 88 sq. km, maximum depth 143 m; mean depth 44 m; volume 3.9 cubic km. The principal part of this Lake is still part of the Swiss midlands. Only its uppermost part reaches into the edge of the Alps. By now man has significantly influenced this Lake. The zones of bulrushes remain preserved only to a very limited extent, and the tributaries of the Lake are in many cases severely polluted by residential and industrial waste.

One should really think that the coregonines of Lake Zurich should have been well-known for decades, for ever since the times of CONRAD GESSNER dozens of Zurich zoologists have devoted themselves to the fish fauna of Lake Zurich. We noted these researchers in the historical chapters of our study, and on this occasion we would merely like to establish that up to the time when FATIO was working on his revision of the Swiss coregonines no uniform and clear opinion concerning the "species" of this Lake was expressed, and FATIO's nomenclature can also not be considered to have solved the numerous tunnels encountered. All in all the coregonine systematics

in Lake Zurich offer additional peculiar difficulties because it has been possible to establish that in historical times considerable changes have taken place, and that these changes were, in part, caused by changes in environment and, in part, probably by the admixture of alien blood.

We know that at the time of KONRAD GESSNER, enormous swarms of dwarfed "hagling" were encountered, a fish which at present appears to have become practically extinct, and we also feel that the larger tribes, in particular the so-called "albeli" have undergone such major changes in the course of the last few decades so that they no longer really correspond to FATIO's descriptions. In addition to this, the ecological conditions have also changed considerably so that today the fishermen of the lakes speak of spawning habits of which nothing was known before.

Let us, first of all, reproduce the opinions put forward by FATIO.

Aside from the "hagling", which we do not wish to examine at present, FATIO distinguishes between 3 larger coregonine tribes which the fishermen of his time designated "blaalig", "albeli" and "bratfisch" ("frying fish").

CONCERNING THE "BLAALIG"

FATIO considered the blaalig to be closely connected to the "blue coregonines" of Lake Constance. The enumeration of trivial names for this type immediately shows a considerable uncertainty in the evaluation of the

species: This fish at that time called "albeli", while in the juvenile stage. Larger specimens were called "blawlig","blaalig", "blauling" or "blaulig"...(Translator's note:--All these names are German or dialect derivations of the word "blue"). FATIO called it Coregonus wartmanni dolosus "âcause des divers aspects trompeurs sous lesquels it se presente à differents âges".

FATIO follows ASPER in considering the "bratfisch" to be a representative of a special species, although fishermen have mostly called it just like the above fish, blaalig, blaulig or blauling, or to differentiate it, occasionally floating or rock blaalig. FATIO called it coregonus asperi maraenoides, and from it he subdivided a further special form which he called Coregonus schinzii duplex, which he, however, stated that the fishermen generally confused it with the "bratfisch".

According to FATIO, the only criterion separating these three kinds of "blaalig" are the gill raker teeth, and we cite his data:

	dolosus	maraenoides	duplex
No. of gill raker teeth	34-39	30-32	26-29

In this connection, the following quotations from FATIO give an indication of the degree of confusion existing at that time: "A great number of hybrids between the dolosus and maraenoides, as well as between the maraenoides and the duplex, can be encountered, since the different types spawn at the same time and in the same location". "Il n'en faut pas davantage pour expliquer l'indécision et les erreurs

des naturalistes qui, tour à tour, ont rapproché le Blauling de Zurich du C. wartmanni, du C. maraena ou du C. féra." On another occasion FATIO directly speaks about a "chaos déjà presque inextricable".

I, for my part, am convinced that if FATIO was able to distinguish between the 3 blaaligs, then he was certainly the only one capable of doing so. I have myself searched for criteria in museum collections, and, more recently, in fresh material, whole series of which were put at my disposal, and I had to admit that this was an entirely hopeless task. The coregonines of Lake Zurich are today, and probably have been ever since time immemorial, a very variable total population, which may perhaps subdivide itself into spawning and age groups swarms, some types of which may live a more pelagic and others a more literal or profunal existence, but the division of which into species appears entirely unjustified.

We now introduce some of the comparative data compiled by us, and we differentiate between the "schwebfelchen", ("floating coregonines"), "bodenfelchen" ("bottom coregonines") and the "albeli" in the manner used by fishermen actually sorting their catch. In this connection, we would like to note that in each case we received material from a certain catch, so that we were entitled to assume that we were investigating the members of a single swarm:

		"Schwebfelchen" ("Floating Coregonines") 20 specimens - 3 to 4 years old	"Bodenfelchen" ("Bottom Coregonines") and "Albeli" caught by means of lake bottom nets
Body Lenth in cm	Maximum	32.0	34.0
	Minimum	26.5	26.5
	Mean	29.3	28.3
Weight in grams	Maximum	260	350
	Minimum	170	140
	Mean	222	194.5
Scale Count	Maximum	97	89
	Minimum	73	78
	Mean	83.3	83.1
No. of Gill Raker Teeth	Maximum	39	37
	Minimum	32	29
	Mean	34.8	32.8

It is, thus, evident that the variation range even in the case of a limited number of individuals examined is considerably broader than one might have supposed according to FATIO. The "types" are by no means clearly separated from one another, but they rather overlap without clear boundaries. In this connection, it might be noted that the series examined by Mr. ED. AMMANN resulted in similar findings, and we thus see no reason for splitting up the big Zurich coregonines into "species" no matter how much the individual tribes may differ in their biological behaviour pattern. A comparison of the measurements based on characteristics which are dependent upon the age, such as the head length, eye size, length of the pectoral fin and the relative compactness, will show the variability of the types even more clearly. We will not reproduce the relevant numerical data here, but we merely state that in analogy to the findings made in late June, young specimens of the individual"tribes" are particularly difficult to differentiate, and also that

all juvenile coregonines have relatively large eyes and heads and tend to have small fins. In addition to this, the juvenile coregonines are slimmer than older specimens, perhaps with the exception of the very oldest age groups, which appear to be characterized by a renewed slimness. The soot marks on the fins are in all cases less prominent in early life than in advanced age. Dwarfed specimens which appear to correspond to "hagling" of earlier centuries and which are still being caught at the corresponding depths today, appear to have juvenile proportions, in particular, large eyes, together with an increased fertility which, in the case of the dwarf coregonines of Lake Zurich, it is marked by particularly dense rows of spawning epidermis. We have dealt with the "hagling" in great detail in a previous publication, and on this occasion we would merely like to repeat that this small fish can still be encountered in some museums and that even today specimens of it could be caught, provided suitable narrow mesh depth nets are used. On the whole this fish corresponds to the dwarf coregonine of Walen Lake, which will be discussed in one of the subsequent chapters.

In the course of a study trip through Switzerland WAGLER has -- as he says --rapidly investigated a number of blaaligs from Lake Zurich. He only realized subsequently that the material investigated by him consisted of floating and bottom blaalig. The sand coregonines could not be clearly separated. Probably WAGLER only realized he mixed up the two types when he subsequently conducted an examination of the gill rakers.

The following is a reproduction of WAGLER's figures concerning the "blaufelchen" ("blue coregonine") of Lake Zurich:

	Gill Raker Teeth																	
No. of Individuals	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
According to WAGLER	-	1	1	1	1	1	2	1	-	-	-	-	5	8	4	2	-	-
According to STEINMANN	1	-	-	-	-	3	3	3	5	7	15	9	12	8	5	2	2	1

For me these very figures clearly indicate that Lake Zurich contains but a single species of coregonines which has become split up into individual tribes which cannot be precisely defined or established. Depending on the location, season, method of catching, etc., one can encounter more of one or of another type within any swarm caught.

CONCERNING THE "BRATFISCH" ("Flying Fish")

As far as we can see, one form is biologically particularly prominent in Lake Zurich, and we may call it the "wanderalbeli" ("wandering albeli"). The name, "bratfisch" ("flying fish") appears to be more suitable to us, although in previous years this name has also been used to designate other partial populations of Lake Zurich.

According to its shape, the "bratfisch" entirely fits within the primigenius group. The detailed structure of the gill raker teeth also supports this classification. Previously the fishermen of Lake Zurich, also called the "bratfisch" roughly "buchberger albeli". As late as the turn of the century, fish of this tribe congregated in September or October in order to pass from the lower Lake

to the upper Lake through the narrows in the dam near Rapperswil. They then continued to migrate in large, wandering swarms without splitting up in the upper Lake until they reached the vicinity of the Linth Canal, when most of them entered the Linth Canal itself. The spawning period can be said to fall within the latter half of December. It would appear that today the wandering coregonine of Lake Zurich grows larger than it did in FATIO's time, but this is probably due to a change in fishing methods which have created an impression of a change, which has no basis in fact. The smaller "albeli" are no longer only exceptionally caught in the presently used wide-mesh nets. They probably returned to Lake Zurich once more only to start migrating upwards again after a period of further growth. There is a divergence of opinion among contemporary fishermen concerning the question of whether the wandering coregonine of Lake Zurich ascends into Walen Lake by way of the Linth Canal. Various reasons make it probable that this upwards migration continues to take place at present at least during warmer years, but in order to be entirely certain, it would be advisable to carry out marking experiments.

Illustration 52: Lake Zurich: "Sandfelchen" ("sand coregonine").

Illustration 53: Lake Zurich: "Hagling" (according to a prepared specimen in the Museum for Natural and Local History at Aarau)

Illustration 54: Lake Zurich: Primigenius,

"Bratfisch" ("Flying Fish"), Linth Canal, Milchner, length 26,8 cm , 155 g, 3 years old.

NOMENCLATURE

We consider the "bratfisch" as we have it ecologically characterized/here to belong to the primigenius group, and according to our practice, we, therefore, designate it: Coregonus lavaretus L. nat. lindimacensis, ecotype primigenius.

In as far as the large coregonines which do not migrate away can be differentiated, we must designate them as follows:

"Floating blaalig": Coregonus lavaretus L. nat. lindimacensis, ecotype pelagicus.

"Bottom blaalig": Coregonus lavaretus L. nat. lindimacensis, ecotype litoralis.

We designate the "hagling" as: Coregonus lavaretus L. nat. lindimacensis, ecotype nanus.

	Circumference	Head Length	Eye Diameter	Caudal Peduncle	Pectoral Fin
"Blaalig"	39-63 Mean 51.3	15-21 Mean 17.1	2.75-5.0 Mean 3.62	5.75-9.5 Mean 7.75	12-19.5 Mean 13.8
"Hagling"	37-58 Mean 49.3	13-19.5 Mean 17.7	3-5 Mean 4.47	5.0-8.75 Mean 7.2	10-15 Mean 13.5

	Scale Count	Gill Raker Teeth
"Blaalig"	69-97 Mean 83.3	27-39 Mean 32.4
"Hagling"	10-15 Mean 84.1	31-33 Mean 31.8

P. GREIFEN LAKE AND PFAFFIKE LAKE

These two small midland Lakes of Zurich kanton are roughly equal in depth and also have similar features in other respects. Greifen Lake is located 439 m above sea level, has a surface area of 8.44 sq. km, and its maximum is 34 m, and its mean depth 19 m. Pfaffke Lake, with an elevation of 541 m above sea level, has an area of only 3.29 sq. km, anaverage depth of 17.9 m and a maximum depth of 36 m. Its volume is approximately half that of Greifen Lake.

In by-gone decades both Lakes were inhabited by autochthonous coregonine stocks, but these have entirely or almost entirely become the victims of progressive eutrophication resulting from the pollution of the Lakes' tributaries. In spite of all efforts on my part, I have been unable to obtain anything but old museum specimens preserved from earlier times for my investigations. In view of these circumstances, our revision can only base itself on very little original data and must be built up on the basis of previously published data.

FATIO places the two "albeli" of Greifen Lake and Pfaffike Lake in the immediate vicinity of the "bratfische" of Lake Zurich. Like the "bratfische" he designates them with the species named Coregonus asperi, to which he adds the designation "sousespèces locales" ("local sub-species") by giving the Pfaffike Lake albeli the name Coregonus asperi sulzeri (nusslin) and the Greifen Lake albeli the name Coregonus asperi dispar Fatio. If we look for differentiation characteristics in FATIO's descriptions, then hardly anything

concrete can be found. It appears that generally the coregonine of asperi type were somewhere in the middle between the floating and sand coregonine types (gill raker tooth count and length were average, the mouth was semi-subterminal, etc.). The figures cited by FATIO were:

	Pfaffike Lake Albeli	Greifen Lake Albeli
Gill Raker Teeth		
1st arch	26-33 cm	22-29 cm
2nd arch	18-25 cm	18-22 cm
Scale Count	87-95 cm	83-90 cm
Length	25-30 cm	24-31 cm
Tail Fin Flaps	Lower usually larger	Mostly equal

The noticeable increase of the weight of the individual fish, which was already noted in the case of other lakes, coregonine stocks of which had become markedly reduced with the passage of years, was equally evident in the case of these two Lakes of Zurich kanton. As the coregonines decreased in numbers, they increased in size. The specimens exhibited in our museums are in most cases also considered to be larger than was to be expected on the basis of FATIO's data. Either museums collected only large, so to say "record" specimens, or the "albeli" of Greifen Lake and of Pfaffike Lake had already reached the size of "large coregonines" by the turn of the century.

Towards the end of the twenties and the beginning of the thirties of this century E. WAGLER came on a study trip from Bavaria to visit the two Lakes, and he had the satisfaction of being able to examine a number of "albeli" both from Greifen Lake, as well as from Pfaffike Lake.

We would merely like to draw attention to the fact that in the course of the last few years repeated introductions of alien fish have taken place. They have certainly not helped to bring about a more uniform coregonine picture. From WAGLER's figures we have only selected the following which we consider significant for our purposes:

		PFAFFIKE Lake	GREIFEN Lake
No. of Gill Raker Teeth	Maximum	37	33
	Minimum	23	23
	Mean	29.8	29.1
Scale Count	Maximum	98	103
	Minimum	76	80
	Mean	88.2	90.7

While it is true that WAGLER calls the "albeli" of both Lakes "blue coregonines" and points out that they have a rate of growth which bears a very close relationship to the blue coregonines of Lake Constance. He, however, adds:

"The blue coregonines of Pfaffikon and Greifen Lakes in their external appearance extremely closely approach the "sand coregonine", even though their growth is typical of the "blue coregonines". Thus, the spaces inhabited by the large floating and bottom coregonines are not separated by too sharp a boundary. It appears quite possible that a partial admixture of the two forms has already taken place in these bodies of water".

We, for our part, would rather say that in these shallow Lakes such a clear differentiation into floating

coregonines and bottom coregonines, such as the one which, for example, has taken place in Lake Constance, could not have taken place.

In any case, it is certain that earlier observers, even those who lived at times when the splitting up into "species" was very fashionable, invariably only knew of one "albeli" for Pfaffike Lake and for Greifen Lake, and that even the professional fishermen working on these Lakes did not use any separate names for the various coregonine tribes. In view of this, it appears much more likely that the fact of a certain differentiation between the floating and the bottom albeli, which WAGLER believes to have observed, can best be explained by considering it to be the beginning of a separation rather than the melting together of two types.

Provided that the rather sparse observation material at our disposal does not mislead us, the phenomenon facing us in these 2 midland Lakes of Zurick kanton is exactly the same as those found to exist in Sempach Lake, Baldegg Lake and Hallwil Lake: An original population of small coregonines in mass swarms, a subsequent decrease in the numbers of the population, together with an increase in weight of the individual fish resulting from the influence of human civilization on the character of the Lake. Simultaneous with this, a gradual transition accompanied by a regression of the typical "floating coregonine" characteristics and an emphasis of the features characterizing shore coregonines. To what extent the introduction of alien bottom coregonines

has played a part in this process is difficult to determine in individual cases. The influence in such Lakes certainly became quite considerable as soon as the autochthonous coregonine population became very sparse.

NOMENCLATURE

The "albeli" of Greifen Lake and Pfaffike Lake must at present be considered to be extinct. In order to rejuvenate the almost entirely disappearing stocks, repeated introductions of "balchen" or "sand coregonines" were made. The old albeli would have had to be designated by the name Coregonus lavaretus L. nat. intermedia, ecotype primigenius.

R. WALEN LAKE

Walen Lake is located at almost the same elevation above sea level as Zuger Lake, i.e., 423 m. It is by far more mountainous than Zuger Lake or the lakes lying at the foot of the Juraf, which also have the same elevation above sea level. Its shoreline is very steep almost throughout its whole length. The mean depth of the Lake is 103 m, the maximum depth 151 m. The volume amounts to 2.5 cubic km. These dimensions make Walen Lake much like Lake Lucerne, to which it is also similar in another respect.

Geologically it can be considered as the uppermost part of the Limmat Valley, and, until relatively recent times, it was connected with Lake Zurich. In a manner similar to the silt deposits from the Lutschin separating Lake Brienz and Lake Thun,the silt deposited by Linth has

created the Linth Plateau which has divided the original unitary Limmat Lake into 2 parts. It is very characteristic that the character of Walen Lake until the nineteenth century was significantly different than its present-day character. According to numerous reports it had an abundant fish population during the eighteenth century. On the whole, it being a Lake of the pre-Alpine region with very steep shores, had features roughly approximating those of Lake Brienz, but while the latter was traversed by the very abundant, and, in summer, muddy waters of the River Aare, the tributaries of Walen Lake up to the beginning of the nineteenth century were relatively sparse (Seez, Murgbach and other small streams).

For a Lake of such dimensions this meant a very low rate of water replacement. At that time the waters of Walen Lake were clear and a rich flora and fuana of organisms had developed there. The free water region, which allowed the passage of light to considerable depths also offered favourable conditions for the development of plankton.

We would like to refer to STEINMULLER, who in 1827 compiled a very diligent study, "Uber die Fische im Walensee und die Fischerei daselbst" ("Concerning the Fish of Lake Walen and the Fisheries there"), During the years 1807 to 1822 ESCHER VON DER LINTH carried out the regulation of the Linth. The Glarner Linth, which previous to this had deposited its silt and rocks in the valley flats between Walen Lake and Lake Zurich, was diverted

through an artificial river-bed to Walen Lake. Even though this new river-bed entered the Lake only some 1.7 km from its drainage point, the glacier waters of Glarus kanton have flown far into the basin of Walen Lake, particularly in summer when its temperature was lower than that of the Lake. Only the upper warmer layers of the water are drained through the Linth canal near Weesen.

STEINMULLER informs us that even in 1800 the coregonine was still the predominating species of fish in Walen Lake. Contemporary fishermen differentiated between two sub-species which STEINMULLER calls, "schwebblauling" ("floating blue one") and "grunder" ("bottom or ground fish"). STEINMULLER considers a third form which other fishermen call "weissfische" ("albeli") ("white fish") to be juvenile coregonines or rather immature "schwebblaulings" or "grunders". The coregonine yield around 1800 was very great. A catch of 100 fish in a day or a night was considered normal for a single fisherman. Around 1700, particularly large coregonine catches were reported during the spawning season. This was said to have taken place between Martin's Mass and Christmas close to the shore of the Lake by means of a special process called "stadnen", (compared also to the "zunden" used to catch "balchen" in central Switzerland). We are told that a spawning ground located within an inlet was surrounded by a net. Then, a fire was started on the shoreline and caused the spawning fish to be chased out into the net. This method of catching "blaulings" was considered the customary property right of the inhabitants of the shore-

line around 1750 and was accompanied by special public celebrations. We know that the fish, which at that time were caught in great masses as was also the case in other lakes, were very much smaller than those presently being caught. The normal size of the "blauling" of Walen Lake hardly ever exceeded 25 cm. The reported weights varied from 125 to 250 gm. Larger fish were a rarity.

According to STEINMULLER "many thousands of hundredweights of all types of fish" died in the years 1813 to 1815. Perch and "blaulings" were primarily affected. The latter were decimated to such an extent that for a few years subsequently not a single specimen could be caught. Starved and dead fishes covered the surface of the Lake. Fish must have really died on a mass scale arousing the attention of a wide public, even outside the immediate area. Only by 1824 individual floating coregonines could again be caught, but their numbers had become significantly reduced in comparison to previous times. STEINMULLER is unable to say anything definite concerning the causes of this catastrophe. He implies that " this calamity must be ascribed to the Linth regulation which caused cold, raw, snow-water from the Linth to enter the Lake, frequently making it muddy, and, thus, bringing about entirely changed water conditions." At the same time it can be assumed that the number of worms, snails and other components of fish nutrition have been reduced as a result of the sedimentation of the materials which caused the Lake to become muddy. This is said to have had

a unfavourable influence upon the health of the fish. Contemporary fishermen thus also explained the poor state of nutrition of the dead coregonine which were found floating on the surface of the Lake during the calamity described above. During the twenties of the nineteenth century coregonine fisheries of Walen Lake were of no practical significance. In only towards the eighties people again began to remember that at one time Walen Lake was said to have been a coregonine lake. From 1888 to 1889 HEUSCHER investigated the biology of Walen Lake and found a great dirth of organisms in its depths. He also found the fuana on the shoreline very sparse, and he was only able to ascertain a minimum of animal life by the rocks on the Lake's shore. While it was true that the plankton of the free-water region was shown to consist of a great variety of species, its actual numerical count nowhere nearly reached that of the plankton in Lake Zurich. This may in part may have been due to the low temperatures, for HEUSCHER found the surface temperature in August to amount to only 17° C. HEUSCHER expressed the opinion that during the last decades of the nineteenth century the Lake, above all, lacked carp-like, small fish, which could have been the nutrition of larger predatory fish. Around the turn of the century A. DORER, in his study entitled "Vom Walenstatter-see" ("Concerning Walenstatter Lake"), published in 1900 in the Swiss Fisheries Journal, reports of several test catches conducted by the enterprising fishing club "See und Gaster" with the help of the net fishermen from Lake Constance.

The results of these investigations were lamentable indeed. Three sets of bottom nets of 30 m gauge, set at depths of 10 to 16 m, yielded 2 small coregonines. Other sets of nets contained no coregonines whatever. To their great surprise, the fishermen did catch a few "rötel". This caused them to express a wish to become acquainted with the spawning places of these fish species, and also to conduct spawn fishing, because experience has shown that "rötel" can only be caught in considerable numbers during the spawning season.

Further experiments were conducted in 1899. Mr. Albert MADÖRIN Sr., Master Fisherman, at that time caught 2 blue coregonines weighing somewhat more than 250 g, and two 3 year old, 21 cm long albeli. His son, Albert MADÖRIN Jr., was interested in the coregonine fisheries of the Lake and decided in 1904 to fish in it systematically. He soon discovered that in the depths of the Lake tiny dwarf coregonines, which one could designate as "albeli" or "haglings" inhabited the depths of the Lake, together with the "rötel". Fishing using bottom nets was particularly favourable in the vicinity of streams entering the Lake at depths of 100 to 150 m. Soon after this MADÖRIN encountered signs indicating that other coregonines, which up to then had not been the object of fishing operations, were also present in considerable number. MADÖRIN introduced sets of floating nets and used various mesh gauges. A floating net having 35 m mesh proved to be suitable, and the yield from that time onwards became quite

good. Two types of yarns were also used successfully. Soon MADÖRIN caught 100 and more fish per day and in isolated instances the draw yarns brought in as many as 1,000 fish in a single day. In subsequent years, good years alternated with less favourable ones, but, generally, no let up in yields could be noted. The last year of MADÖRIN's concession was an outstanding year for yield. One catch of 60 fish was considered normal for one set of 20 floating nets 80 m long. A yarn net delivered 10 to 15 fish per day, although mass catches of 300 to 400 fish also took place.

The floating coregonines of Walen Lake, which we again wish to designate as "blauling", were marked by a fairly uniform size and a weight from 250 to 300 g, and they were relatively slim. This type continues to be well represented in the Lake to this day. Using short yarn nets MADÖRIN was also able to catch numerous sand coregonines. MADÖRIN did not particularly devote himself to spawn fishing. He found that the "land balchen", that is to say, the sand coregonines spawning on the shore did so until the end of November and beginning of December, but he did not disturb them. He states that the spawning season of the floating coregonines was in February, and, according to him, these fish spawned at depths ranging from 100 to 150 m. Among the "albeli" MADÖRIN differentiated between the "summer albeli" whose spawning season took place in August and September, and the "winter albeli" whose reproductory period coincided with the coldest season of the year. MADÖRIN caught the small

coregonines with relatively fine nets having a mesh of some 24 mm. He, however, took care to refrain from using such nets close to shore, since this would have resulted in large quantities of floating coregonines and sand coregonines becoming mixed in his catch.

In 1927 MADÖRIN decided after 23 years of work to give up any further fishing in Walen Lake and moved back to Lake Zurich. The fisheries at the former were again taken over by local fishermen. Ever since 1933 the yields have been statistically recorded. We will return to these figures later.

For obvious reasons, the activities of the Zurich fisherman, MADÖRIN, were not viewed upon with favour by some local inhabitants. It seemed unbelievable that a lake which previously had been considered as unproductive suddenly provided not only good but also repeated good yields. As a result, people talked about "robbing out" the Lake, but in actual fact the yields in the course of these 23 years did not decrease but increased. In a deep lake of the type of Walen Lake special knowledge and experience and constant observations are particularly needed in order to assure yields corresponding to the actual fish population. We are convinced that in other bodies of water too a maximum utilization of the available fish resources has by no means been achieved.

The Coregonine Types of Walen Lake, Their Peculiarities in Shape, Growth and Living Habits

The Geneva scientist, FATIO, towards the end of the last century only knew of a single "coregonine species"

from Walen Lake. He designated it with the name "albeli-blauling". The period of his researches coincided with the time during which no serious coregonine fishing operations whatever took place. In 1899, on the hand, DORER differentiated among no less than 6 different "species" which he called: "blaufelchen" ("blue coregonines"), "sandfelchen" ("sand coregonines"), "gangfische" ("wandering fish"), "kropffelchen" ("goiter coregonine"), "winter albeli" and "summer albeli". DORER appears to base himself on several professional fishermen, who at that time came from other lake districts from eastern Switzerland for test catches to the Lake, and who believed to recognize the types known to them from their native waters in the few coregonines they caught in Walen Lake.

In the years 1938 to 1940 and again later, I had myself investigated coregonines from Walen Lake when I had the opportunity to do so, and I arrived at the conclusion that it is possible to differentiate between 4 types, one of which should be further subdivided ecologically. I differentiate between:

1. The "floating coregonine"
2. The "bottom coregonine"
3. The "albeli"

The latter local race can be subdivided at least into summer and winter albeli if one takes their spawning season into consideration. It also appears that there is a further special tribe of medium growth found in the free water regions of the Lake which could perhaps be subdivided

as "floating albeli". We will deal with this type in greater detail further on. To this there should be added -

4. A Primigenius,

which we will designate "bratfisch".

1. The "floating coregonine"

The floating coregonine of Walen Lake as it is presently encountered is very clearly different from the blue coregonine of Lake Constance. Blue specimens are hardly ever encountered. The fish are almost invariably olive green to brownish in colour. Their weights vary depending on which age groups predominate. At present larger types predominate in the catches. In September, 1949, we were able to find specimens measuring 42 and 43 cm and weighing from 650 to 780 g. They were 5 to 6 years old. In spite of their relatively scarce available numerical data, we feel can publish the following values:

3 year olds.....25-32 cm
4 year olds.....30-37 cm
5 year olds.....35-43 cm
6 year olds.....37-43 cm

This coregonine is considered primarily to feed itself on plankton. Its gill rakers are fairly long, their number vary from 31 to 38, their mean being 34.1. As a result the gill filter is not as fine as that of the blue coregonines of Lake Constance and more closely approaches that of the Primigenius type. We know little concerning the spawning habits of this fish. It is, however, certain that it does not spawn close to the shoreline. It appears probable

that towards late autumn it moves to the depths of the Lake and that it spawns during the winter. MADÖRIN suspected that the floating coregonine spawned in February. So far it has not been possible to catch any considerable number of fish during their spawning maturity so that to this very day it has been impossible to use the Walen Lake floating coregonines for the usually practiced artificial breeding operations. The catches are most abundant in May. Generally it is figured that during this season the upper 30 m can be considered to be the habitat of the floating coregonines. From June onwards they appear to come somewhat closer to the shore, but there are differences of opinion among individual fishermen concerning this matter. Generally, it has been observed that at certain times yields suddenly get poor without any definite known reason. MADÖRIN put the blame on strong under-water currents and temperature differences caused by sudden climatic changes, and he presumed that the coregonine swarms which at times were compact suddenly loosened up and then moved to entirely different depths in the Lake. One interpretation of this phenomena, namely, that the coregonine stocks at such times had died out or had been exhausted through fishing operations, an opinion which, incidentally, is heard over and over again from fishermen, can be considered invalid if for no other reason than simply because the very age groups which appear to be missing are frequently caught in considerable numbers during the following year when they have joined together once more. I once received an entirely mature and one entirely immature male in December. I do not know the duration of the spawning period, nor do any of the fishermen anything positive concerning

the localities at which catcheswere made during the spawning period.

2. The Sand Coregonine ("Ground Fish")

This type corresponds to STEINMULLER's "grunder". The shape of its body is somewhat more compact than that of the floating coregonine. The head is smaller, and the snout usually appears somewhat dull. As far as we are able to judge, the sand coregonine has a somewhat better rate of growth than the floating coregonine. Occasionally specimens weighing also 2 kg were caught. We are not particularly well informed concerning the locations of the pastures throughout the year. The sand coregonines appear to live either close to shore or also at greater depths. The stomachs of the specimens investigated by me contained mainly snails, worms and insects. From the middle of January onwards sand coregonines are occasionally caught in so-called land-yarn nets. Nevertheless this fish does not appear to be too plentiful anywhere and it probably lives well distributed, and thus a yield of 20 sand coregonines in a single land-yarn net is considered quite favourable. Thus, the "grunder" lives a more or less isolated existence. Every individual independently seeks his nutrition. They only join in swarms during the spawning period. The latter is relatively short and last from approximately November 15th to the beginning of December. The spawning grounds are close to shore. Deposits of larger rocks at the edge of the Lake and the like are preferred. At the right shore of the Lake close to Quinten catches are particularly plentiful, but spawning "grunders" are also caught at various

spots on the left shore of the Lake. At present "grunder" spawn is primarily used for artificial fish breeding. Fishermen declare that this has been worthwhile, and have in the course of the last few years lead to an increase in the number of "grunders". In conclusion we would like to give a few figures to characterize the "grunder":

No. of gill raker teeth on the first gill arch: 24 to 28, with a mean of 25.8.

Eye diameter in percent of head length: 3.1 to 3.8%, with a mean of 3.5, in which connection it should be noted that only larger specimens were measured.

Circumference in percent of body length: Always exceeding 50%, mean of 16 individuals measured: 54.5%, maximum 61%.

The sand coregonine appears to have a somewhat shorter tail than the other races. The mean amounts to 7.07%. The fact that a 3-year old specimen already measured 37 cm, 5-year old on the average 41.6 cm and 8 and 9-year old ones almost 50 cm, bears testimony to the good rate of growth of the "grunder". The scales tend to be somewhat smaller than those of other races. Within a variation range of 82 to 98, the mean was found to be 90 scales along the lateral line.

3. The "Albeli"

As early as 50 years ago the "albeli" of Walen Lake were divided into "summer albeli" and "winter albeli". Upon examining a considerable number of these fish, we have not been able to detect any noticeable differences in the

body proportions or the gill rakers, and even the rate of growth, no matter how variable it may be, shows hardly any difference between the summer and the winter albeli. If there is any difference at all, then it is in the size of the scale. While the winter albeli has a scale count varying from 70 to 85 with a mean value of 76.6, that of the summer albeli varies from extreme values of 76 to 106, with a mean of 84.7. We found no significant difference in the eye size, the length of the pectoral fin or that of the caudal peduncle. Thus, we are faced with the fact that 2 tribes of almost identical morphology are biologically different in that one tribe spawns from July to September, while the other does so from December to February. Some 12 fully grown fish which have reached spawning maturity weigh 1 kg. The winter albeli were still unknown during the last century. Prof. HEUSCHER was sent his first specimen in 1899. He emphasized that 2 years previous to that the same type of coregonine had been discovered in Lake Zurich. This indicates that we should be able to connect the albeli of Walen Lake with the frequently discussed "hagling" of Lake Zurich. While the "hagling" of Lake Zurich must today be considered practically extinct, it continues to live and thrive in Walen Lake and even appears to be quite numerous there. Being a true dwarf race, the "albeli" are extraordinarily fertile. One of the results of this is that fact that subsequent to reaching their spawning maturity during the third year of their lives, in the case of males as early as the second year, they no longer grow at any worthwhile rate. The nutrition of the

albeli consists in part of plankton, but in part also of insects and mollusks. As far as we are able to judge at present, the summer albeli differed from the winter albeli to a certain extent in their nutrition. During summer catches I repeatedly found plankton in the stomachs of the immature fish, while finding bottom nutrition in the stomachs of "bottom albeli" approaching maturity (pisidae, chironomidae larvae). I have gained the impression that the winter albeli primarily keep to the pelagikum, and are then frequently caught by means of floating nets, provided the mesh of the latter is suitable. I would, on the other hand, like to consider the "summer albeli" as deep water fish, who, similar to the "weissfishchchen" ("little white fish") are drawn up from great depths during the summer. The
which it is possible to observe to a particularly marked extent and very frequently in this race naturally reminds one of the "kilch" and the "kropfer". I, however, find the latter 2 to be profundus ecotypes originating from shore coregonines, while the small deep water fish of Lake Lucerne and Walen Lake appear to go back to a floating form. These little fish also have little in common with the "gangfisch" ("wandering fish") of Lake Constance. In this connection, it would merely be pointed out that the albeli spawns at considerable depths, generally speaking, never is seen in shallow waters.

4. The "Bratfisch" ("flying fish")

In 1949 we for the first time obtained possession of several medium sized coregonines characterized by the first signs of approaching secual maturity, while floating

coregonines and "grunder" of the same size, caught simultaneously, were still immature. The external appearance of these fish reminded us of the "white coregonine" of Lake Constance and the "bratfisch" of Lake Zurich, which we have characterized as "wandering albeli". For the time being we assume that this is the "albeliblauling" ("blue albeli") which FATIO has designated as Coregonus wartmanni dolosus, and we, therefore, classify it as the typical "original coregonine" of the Limmat region and a member of the "Primigenius class".

Comparison of the Coregonines of Walen Lake with those of Lake Zurich

The "grunder" entirely corresponds to the "bodenblaalig" ("bottom blue") and belongs to the "litoralis" group. The "schwebblaalig" ("floating blue") of Lake Zurich has its counterpart in the pelagicus ecotype of Walen Lake, which is called "schweber" ("floater"). An intermediate tribe which has been designated by various names including such names as "floating albeli" by the fishermen, which, however, best should not be called "albeli", corresponds to the "bratfisch" of Lake Zurich, and the term "hagling" could be used to designate the "albeli" of Walen Lake. With the "winter albeli" perhaps being characterized as "nanus", and the "summer albeli" or "bottom albeli" could be called "profundus".

NOMENCLATURE

"Grunder": Coregonus lavaretus L. nat. lindimacensis, ecotype litoralis,

"Schwebblaalig": Coregonus lavaretus L. nat. lindimacensis, ecotype pelagicus,

"Bottom Albeli": Coregonus lavaretus L. nat. lindimacensis, ecotype profundus,

"Floating Albeli": Coregonus lavaretus L. nat. lindimacensis, ecotype nanus,

("Bratfisch"): Coregonus lavaretus L. nat. lindimacensis, ecotype primigenius.

Walen Lake

	Circumference	Head Length	Eye Diameter	Caudal Peduncle
Albeli	41-59 Mean 51%	16-20 Mean 18.1%	3.6-5.7 Mean 4.7%	6-9 Mean 7.7%
Floater	46-58 Mean 52.9%	16-18 Mean 17.1%	3.2-4.6 Mean 3.86%	6.5-9.5 Mean 7.8%
"Grunder" (roughly, "ground fish")	51-61 Mean 54.5%	14.5-17.5 Mean 15.9%	3.1-3.8 Mean 3.5%	6-9 Mean 7.1%

	Pectoral Fin Length	Scale Count	Gill Raker Teeth
Albeli	S. 13 -18, Mean 14.7% W. 13.5-19.5, Mean 15.0%	76-106, Mean 84.7 70- 85, Mean 76.6	29-42, Mean 35.4
Floater	13-15, Mean 13.6%	76-89, Mean 81.3	31-38, Mean 34.1
"Grunder" (roughly, "ground fish")	12-15, Mean 13.4%	82-98, Mean 90	24-28, Mean 25.8

Illustration 55: Walen Lake: "Floater".

Illustration 56: Walen Lake: "Grunder" (Roughly, "Ground Fish").

Illustration 57: Walen Lake: "Floating Albeli".

Illustration 58: Walen Lake: "Depth Albeli".

S. THE KLÖN VALLEY LAKE

One of the lakes which has only become a coregonine lake as a result of recent introductions of coregonine stock is the Klon Valley Lake in Glarus kanton.

The surface of the original Klon Valley Lake was 832 m above sea level. It had the following dimensions: Length 2.75 km, width .65 km, area 1.307 square km, volume 10 million cubic m, depth 20 to 33 m. In 1908 the Lake became a part of a dam system. Since then the lowest level of the Lake has been 827.8 m, the highest level 850 m, more recently 851 m. As a result of the dam, the new Lake has a volume of 45 million cubic m. At such times its area is 3.417 square km, that is to say it covers a considerably greater portion of the valley than it did previously.

On the basis of an investigation conducted in 1906, J. HEUSCHER of Zurich expressed himself on the subject of fisheries in Klon Valley Lake. He advised the introduction of coregonines (from Pfaffike Lake).

In the period from 1905 to 1919 with certain interuptions, some 50,000 coregonine fry were planted each year, which amounts to some 500,000 fish in 10 such campaigns.

From 1914 to 1918 annual catches of 50 to 150 fish were recorded. These catches were limited to the spawning period.

In 1928 the Federal Inspector of Fisheries again recommended the introduction of coregonines after various signs had indicated the success of the original stocking experiment. During these years there is reference to a "constantly increasing coregonine population", and H. WILD reports in his "Memorial Publication on the Occasion of the Fiftieth Anniversary of the Glarus Fisheries Association" about coregonine catches using bottom lines with worm lures. From 1928 onwards proper fishing

operations were initiated in Klon Valley Lake, and every year thereafter several hundred thousands of coregonine fry, in 1938 no less than 830,000, were introduced in the Lake. Ever since 1937 a good part of these originated from spawning catches from the Lake itself. The coregonines obtained from the "Konkordat" Association probably originated, at least in part, from Walen Lake, and, in part, from Lake Zurich.

The use of local spawn was connected with certain difficulty, because the Lake occasionally froze over before the fish had achieved spawning maturity. Fishermen also reported that the coregonines did not achieve maturity simultaneously. Yield is reported to have dropped off somewhat in the course of the last few years. Frequently fishermen report catching coregonines which have been bitten by pikes. A test catch conducted in 1943, however, showed that the Lake continues to contain quite a satisfactory population of large and small coregonines. In the course of two weeks, one set of floating nets and several bottom nets brought up 54 large coregonines, 255 "small coregonines" weighing 100 to 300 gm. Fisheries supervisors declared that the catch consisted almost exclusively of "blue coregonines" with a few "albeli". In the opinion of fishermen, the present-day coregonine population is so good that angling for pike and perch is becoming less successful. These predatory fish are said to have so many coregonines at their disposal that they no longer bite at the bait offered to them. H. WILD consequently also suggests the increased use of bottom nets and bottom angles in coregonine fishing -- from a scientific point of view we would be interested in solving the question of any possible change in the coregonine population since the beginning of the acclimatization

of alien fry.

Unfortunately it is difficult at present to determine the origin of the coregonines first introduced 40 years ago. One can, however, assume with certainty that they included coregonines from Walen Lake and Lake Zurich, and that probably these were recommended by the "wandering albeli", also called "bratfisch", which I count as belonging to the "primigenius race" and which were raised in great numbers by the "Konkordat Association" hatcheries.

From the age of the individual size and weight groups a good rate of growth could be deduced. This was also the case in the instance of Lungern Lake, which is some respects is similar to Klon Valley Lake.

NOMENCLATURE

For the time being we consider the Klon Valley Lake coregonine to belong to the Primigenius group, and we, therefore, designate it: Coregonus lavaretus L. nat. lindimacensis, ecotype primigenius.

T. LAKE CONSTANCE

The "Swabian Sea" is the second largest lake of the territory investigated by us. It is located 399 m above sea level, that is to say practically the same elevation as that of Lake Geneva, which, however, exceeds it in area and in particular in depth. The surface area of Lake Constance amounts to 538 square km, maximum depth 252 m. Since it also includes shallower waters, its mean depth is only 99 m, and in

this respect it is surpassed by 10 other lakes in our country. In view of this, its volume also amounts to only a little more than half that of Lake Geneva, namely 48.4 cubic km.

For our purposes the form of Lake Constance, i.e., its division into two quite different basins, namely a shallow, lower lake and the deep, upper lake, is particularly significant. We will have to show that the fish in these 2 sections, which are connected by the short "Lake-Rhine" stretching from Constance to Gottlieben, are significantly different in various respects. Thus, the coregonines of both sections of the Lake present a clear picture of the influence of environment. In this connection, we are thinking less of actual modifications, but rather of race selection. We will return to this matter in the last part of our study.

Published data dealing with the coregonines of Lake Constance is extraordinarily voluminous. In this respect, this body of water passes all other lakes of our territory. If, therefore, Lake Constance can be considered the most thoroughly investigated of our coregonine lakes, we are still by no means entitled to consider all problems connected with this Lake as being solved. The coregonine types of Lake Constance have all be subjected to monographic treatment to a greater or lesser extent, and attempts have been made on this basis to identify them with the coregonines of the other lakes. When we first began our investigations we also set out from this point of view. It appeared natural to us to use the prior work of so many fellow specialists as our point of departure and only relatively late did we realize that a basic revision was called

for. For this reason, that section of our coregonine monograph which deals with Lake Constance also turned out to be the most detailed one.

The coregonine population of this Lake is in part composed of quite different types, and their differentiation presented not only fishermen, but even experts, with many difficulties. The most important stages in this history of exploration have already been described in the historical section of our study. Rather than repeating them, we will start with the findings characterized by WAGLER in his "Handbuch der Binnenfischerei Mitteleuropas" ("Manual of Central European Inland Fisheries") and other publications in the thirties of this century. According to these findings, there are 4 "species" of coregonines in Lake Constance. We will briefly characterize them according to WAGLER's data:

Blaufelchen ("Blue Coregonine")

Gill rakers: 30-40, long and narrow. Back in most cases has bluish colouring, occasionally also pale. Fins of matured fish more or less blackened, particularly the pectoral fins. Eye not particularly large, approximately 3.5% of the body length. A fish of the free water regions, short spawning period (floating spawner), beginning of December.

Rate of growth: 1. 10; 2. 20; 3. 28; 4. 34; 5. 38. Nutrition: Plankton, floating insects.

Gangfisch ("Wandering Fish")

Gill raker teeth: 35 to over 40, long to very long. Colouring of back, tail olive, occasionally bluish-green. Fins only slightly blackened, whitish, yellow to redish. Eye

large, approximately 4% of body length. A fish of the free water regions, but less frequently out in the open Lake, but rather closer to shore. In shallow waters, also further away from shore. Nutrition same as blue coregonine, but greater emphasis on insect nutrition. Extended spawning period lasting from late autumn into January. Bottom spawner.

Rate of growth: 1. 9; 2. 17; 3. 22.5; 4. 26.5, 5. 30.

Sandfelchen ("Sand Coregonine")

Gill raker teeth, 20-30. Colouring of back bluish green to more or less olive coloured. Pectoral fins as well as other fins only slightly blackened. Eye small, 3.3% of body length. Head compact, snout blunt, mouth subterminal. Intermaxilla sloping diagonally back and downwards. Habitat: Near submarine elevations or close to the bottom. Nutrition: Mostly animals from the lake bottom, in particular shells and snails. Spawning period short. Spawning location flat shores, occasionally also running water.

Rate of growth: 1. 10.8; 2. 23; 3. 32.5; 4. 38; 5. 43.

Kilch

Average gill raker count, less than 25. Very short. Colouring, very pale, brownish olive. Pectoral fins, white, and remaining fins hardly blackened or not blackened at all. Eye large, approximately 4.5% of body length. Head long, but wide. Snout, blunt, mouth always subterminal. Intermaxilla, sloping sharply downwards and backwards. A fish

inhabiting the depths close to the bottom. Nutrition: Predominately animals from the lake bottom, such as snails and shells. Spawning period extensive lasting from summer into autumn. Eggs invariably deposited in the depths.

Rate of growth: 1. 9.5; 2. 17; 3. 22; 4. 26; 5. 29.

On the basis of our own experiences we would have to take certain exceptions to WAGLER's above diagnosis, but we merely refer to the detailed explanations which will follow. Nevertheless it should be emphasized that in particular we by no means agree with the colouring characteristics since we have been able to get an entirely different impression on the basis of observing freshly caught and still living material. Thus, for example, the "sand coregonines" of Lake Constance (we have personally examined specimens from the Upper Lake and the Lower Lake) are characterized by dark fins and three-year old and older typical "gangfisch" ("wandering fish"), as well as "kilch" have strongly blackened fins when the living fish is first brought to the surface. The fact that WAGLER's data concerning nutrition does not correspond to our findings may be a result of WAGLER conducting the stomach investigations only at certain seasons of the year. In this connection, we would merely like to point to the masses of young perch swallowed by "blue coregonines", and, further, the plankton nutrition which is occasionally encountered in the stomachs of "sand coregonines". In particular, we must at this stage emphasize that we really don't know what to do with WAGLER's "rate of growth average values", since we kept on encountering greater

differences in the populations investigated by us, and these greater differences indicated a really unbelievable "growing apart" of the coregonines.

We consider the diagnosis given above as misleading. It won't even enable an expert to classify any specimen caught in Lake Constance with any degree of certainty. They would become entirely unsuitable if we were to do what WAGLER does, namely to apply his differential diagnosis to coregonines of other lakes. One simply has to take the trouble to check and sort the many hundreds of coregonines being received at Staad, Langenargen or Ermatingen at such times as during the main marketing season. Anyone, even the most knowledgeable expert and the acutest observer, would be haunted by outs. Along with "typical" "blue coregonines" "wandering fish" or "kilch" entirely atypical specimens are encountered, and they cause the fishermen and fisheries supervisors to engage in a proper guessing game. Finally, someone shrugs his shoulders and the magic word "hybrid" or "bastard" is pronounced, thus expressing the opinion that the specimen in question is an intermediate or transition type, a mixed form. Even though it must be admitted that mutual cross-breeding between different coregonine races may take place under natural conditions, it should never be forgotten that the spawning periods and spawning grounds of the typical coregonine tribes are very different. In view of this, it is unthinkable that hybrids or bastards should be created in such numbers and should survive so well that occasionally they actually predominate in individual populations. In view of this and in view of a number of other considerations, we felt that the intermediate form which kept

reappearing in the course of our investigations, should be assigned a systematic classification of its own, and we decided to establish the "weissfelchen" ("white coregonine") as a special race which is quite numerous in Lake Constance, and, in particular in Lower Lake. We would like to refer to our study published in the "Zeitschrift für Hydrologie" ("Journal for Hydrology"), Volume 10 (1948), and entitled "Der Weissfelchen des Bodensees und die Frage der Artbildung im Felchengeschlecht" ("The White Coregonine of Lake Constance and the Problem of the Creation of Species Among the Coregonines"). We certainly don't want to omit stating with the greatest possible emphasis that the old experienced on Lake Constance had made this separation a long time ago, and that the "white coregonine type" also called names such as "silberfelchen" ("silver coregonine") keeps reappearing in the literature of earlier decades. Thus, for example, Mr. LAÜBLI Sr. at Ermatingen, in a publication entitled "Internationale Fischereiausstellung Berlin, Katalog der schweizerischen Beteiligung" ("International Fisheries Exhibition Berlin, Catalogue of the Swiss Participation"), published in 1888, listed the "weissfelchen" ("white coregonine") of Lake Constance as a separate type occurring in great numbers in the Lower Lake and infrequently in the Upper Lake. A weight of 1 kg was said to be no rarity for this fish. The "gangfisch" ("wandering fish") never achieved this size, but only 300 gm at the most. This entirely corresponds to the data supplied by Mr. KOCH, a fishermen from Reichenau, who just as his Swiss colleague, supports the separation of a "specific weissfelchen"

("white coregonine") or "silberfelchen" ("silver coregonine") which differs both from the "sandfelchen" ("sand coregonine") as well as the "gangfisch" ("wandering fish"). This opinion was last expressed in a publication entitled "Das Fischereigewerbe und der Fischfang in den einzelnen Monaten des Fahres im Untersee" ("The Fishing Industry and Catches Brought In From Lower Lake in the Individual Months of the Year") (1928). It is noteworthy that WAGLER too occasionally mentions the "silver coregonine" of Lower Lake, even though he classifies it together with the "sand coregonine", even though its characteristics show a not inconsiderably deviation from those of a typical "sand coregonine" according to WAGLER's own tables. This published data at one time caused me to reinvestigate this question in years 1947 to 1949. As a result I separated and characterized one coregonine type which must be considered to be a fifth "race" of Lake Constance. We will deal with this type first.

THE "WEISSFELCHEN" ("White Coregonine")

Characterization

In conjunction with our above-mentioned study and using further new studies on the site, that is to say, directly on Lake Constance, and, in particular, on Lower Lake, we compiled those characteristics of the Coregonus bodanensis primigenius which appeared significant to us:

A coregonine form which is neither particularly slim, nor clearly compact, and has a light, as a rule slightly brownish or brownish-olive basic colour. The fins of younger fish are yellowish or orange, those of older fish become severely

blackened. The head is blunter than that of the "gangfisch" and the mouth is almost terminal. Old specimens are somewhat plump and clearly compressed laterally. Young specimens appear to be slimmer.

The great variability in the scale count is very evident. The variation range can be seen from the following table:

70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
1	1	3	1	--	--	2	1	2	1	5	9	8	8	17	10	10	10	18	14	9

91	92	93	94	95	96	97	98	99
13	3	2	1	--	--	--	1	1

In the number of gill rakers the "white coregonine" is in the middle between the other races:

24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
2	3	4	5	14	10	12	11	12	13	17	17	22	21	20	8

Since the material sent to us for investigation contained both large and small coregonines, the variation ranges of the relative head length and relative eye size are quite considerable:

Head Length Expressed in Percent of Body Length

15.0	15.5	16.0	16.5	17.0	17.5	18.0	18.5	19.0	19.5
2	1	16	34	43	35	35	27	12	3

20.0	20.5	21.0	21.5	22.0	22.5	23.0	23.5	24.0	24.5
3	3	1	--	--	2	1	--	--	1

Eye Size Expressed in Percent of Body Length

3.0	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8	3.9	4.0
2	2	1	3	7	9	8	13	15	19	13

4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8	4.9	5.0	5.1
16	17	17	10	6	6	3	3	5	4	1

Pectoral Fin Length Expressed in Percent of Body Length

10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0
1	1	6	11	30	35	32	25	15	15	6	4	--	1

Circumference Expressed in Terms of Percent of Body Length, Co-efficient of Slimness

44.0	44.5	45.0	45.5	46.0	46.5	47.0	47.5	48.0	48.5	49.0	49.5	50.0
1	1	--	2	1	2	7	7	4	5	5	8	6

50.5	51.0	51.5	52.0	52.5	53.0	53.5	54.0	54.5	55.0	55.5	56.0	56.5
6	10	9	6	5	2	3	2	2	3	2	3	2

57.0	57.5	58.0	58.5	59.0	59.5	60.0	60.5	61.0	61.5	62.0	62.5	63.0
1	3	--	--	2	2	--	--	--	--	1	1	--

The distribution of the "white coregonine" in the Lake Constance area is by far greater than was hitherto assumed. Some fishermen believed that this race was entirely or almost entirely limited to the Lower Lake, and various scientists, including KLUNZINGER (1892) state that the fishermen of the Upper Lake only know the "sand coregonine". In the Lower Lake, on the other hand, professional fishermen differentiate a special "white coregonine" or "silver coregonine" which achieves

a maximum weight of 1 kg and spawns along submarine mountain ranges during the second half of November and which must be considered to be a frequently encountered inhabitant of these waters. KLUNZINGER does, however, have to admit that relatively large silver-coloured coregonines are occasionally also caught in the Upper Lake, and he in particular mentions such catches at Immenstaad where a wide mesh net can be set on rocky ground in shallow water to catch these so-called "adelfelchen" ("nobility coregonines"). I, for my part, have heard several fishermen state that such silver coregonines are caught in the Upper Lake all the way up to Lindau and Bregenz. It appears that this fish tramps about in a great variety of biotopes. Occasionally individuals join swarms of blue coregonines and are caught together with them in yarn nets, but according to our own experiences the mounds and hills underneath the water's surface close to shore are a more usual habitat of the "white coregonine". We encountered it at Uberling Lake in the vicinity of Ludwigshafen in the company of old blue coregonines. It was also found at Langenargen, and Dr. NUMANN has repeatedly sent me material for investigation. Young specimens which fishermen call " yellow or brown coregonines" and which can easily be confused with "gangfisch" ("wandering fish") at the first glance can be encountered near Kesswil, Romanshorn and Rorschach. Their lengths vary from 25 to 28 cm. Probably these are swarms of "white coregonines" whose urge to migrate has been demonstrated over and over again.

"White coregonines" in great numbers are caught in the shallower zones of the Lower Lake in Gnaden Lake and

in the direction of Radolfszell. Swarms of "braunfelchen" ("brown coregonines") or "Brunner-felchen", thus called after a fisherman for whom catching this race had become a speciality, are near Kressborn and Lindau. All these must be considered to be "white coregonines". Mr. HIRN, Fisheries Superivisor at Lindau, let me have several specimens during the spawning period. They clearly differed from the "gangfisch".

In order to avoid many misunderstandings, a remark should be made concerning the name "silberfelchen" ("silver coregonine"). At present this designation is misleading because in the fish trade it includes all coregonines except the "blue coregonines", i.e., "gangfisch" ("wandering fish"), "kilch", "sandfelchen" ("sand coregonines"), "weissfelchen" ("white coregonines"). If one makes detailed inquiries, it becomes evident that many fishermen know quite a bit about all these details, but they pay little attention to them since the trade which uses the term "silberfelchen" ("silver coregonine") does not recognize these differences. Juvenile coregonines also frequently are very similar to "kilch" of the same size. The characteristic feature in all cases is the almost terminal mouth and the gill raker apparatus. Their differentiation of juvenile "white coregonines" from "gangfisch" of the same size is occasionally more difficult. As we explain elsewhere, we consider the "gangfisch" to be merely a tribe of "white coregonines" with dwarfing tendencies, and, thus, we again approach the earlier views of KLUNZINGER, who at one time indulged in long discussions and polemics concerning this problem with NUSSLIN.

The spawning period of the "white coregonine" is some two weeks to 20 days before that of the "gangfisch". The spawning grounds are shallow waters close to shore, and in part also the flowing waters in the uppermost region of Lower Lake near Gottlieben-Ermatingen, in other words, locations which towards the year are also visited by the dwarf tribe, the "gangfisch". In part, the "white coregonines" also tend to spawn further away from shore and at somewhat greater depths than the "gangfisch".

As far as the rate of growth of the "white coregonine" is concerned, it is roughly in the middle between the "blue coregonine" and the "gangfisch".

In conclusion it can be stated that the "white coregonine" belongs somewhere in the middle between the 2 extremes characterized by the floating and the bottom fish, and that it is similar to the "albock of Lake Thun, the "balchen" of Zuger Lake, the "balchen" of Lake Lucerne, the "palée" of Lakes Neuchatel and Bienne, and the "féra" of Lake Geneva, as well as other forms found in Swiss Lakes. We consider the "white coregonine" to be a primitive not differentiated form among the coregonines and to be quite close to the "original coregonine" the hypothetical original inhabitant of our territory.

This also finds its expression in its living habits. Its nutrition is composed of quite varied components. The stomachs contain plankton as well as bottom nutrition, just as is the case with the "palée" and the "féra". Their race is characterized by a pronounced migratory urge. As a result, fishing for "white coregonines" is subject to many elements of

chance. Unfortunately, the usual fishing methods presently practiced by the fishermen of Lake Constance are of little use in helping us clear up the overall picture of the distribution of the "white coregonine" and its relative frequency among the population of the Lake. The "segi" type net, which would probably bring more of these fish to the surface, is used in the Upper Lake only on exceptional occasions when the "blue coregonine" catches are unsatisfactory. During that period the professional fishermen like to direct their attention to the pikes and perches in the Lake, so that the "white coregonine" only becomes an incidental part of the catch in September and October. Conditions are different in the Lower Lake, where the part played by the "white coregonine" almost corresponds to that of the "blue coregonine" in the Upper Lake. This is the case during the summer months, and particularly also during the spawning season in November.

The "Blaufelchen" ("Blue Coregonine")

The "blue coregonine" of Lake Constance is the most thoroughly investigated coregonine race. In his "Attempt at a Monograph" entitled "Der Blaufelchen des Bodensees" ("The Blue Coregonine of Lake Constance") WAGLER (1927) mentions no fewer than 131 studies dealing with this fish. As early as in 1777 B. WARTMANN, a physician from St. Gallen, wrote a "Beschreibung und Naturgeschichte des Blaufelchen" (" Description and Natural History of the Blue Coregonine"), which in its time was an example of a good ecological study. There is no lack of shorter or longer descriptions of this well known fish. Nevertheless it is not easy to obtain a clear unequivocal

picture of the "blue coregonine" since it, like all coregonine races, is very variable. We entirely agree with WAGLER when he points out that even well-trained, experienced fishermen cannot differentiate between the "gangfisch" and the "blue coregonine" with any degree of certainty. Both he and I have encountered instances over and over again in which, as WAGLER expresses himself, "a hunch plays a more decisive role than positive knowledge".

Let us start with the colouring which is the best differentiation characteristic for the layman. Blue coregonines: Greenish-blue colouring of the back; Gangfisch: Light olive brown. Among hundreds of blue coregonines I repeatedly also saw paler ones. The "blue coregonine", like all coregonines, can change its basic colouring in a short period, even in the course of its presence in a floating net, but particularly after death. Living and entirely fresh blue coregonines generally have the characteristic colouring, but only a minority of researchers obtain the fish in this condition. According to NUSSLIN, the sides of the head of the blue coregonine are light, while those of the "gangfisch" are darker. To this WAGLER remarks that this feature is by no means reliable, and SCHEFFELT and SCHWEIZER emphasize that the colouring of the head varies considerably. In the summer of 1949 I, together with AUERBACH and MUCKLE, undertook several trips on Upper Lake and I have also studied the fisheries of the Lower Lake right on the spot in order to be able to examine freshly caught "blue coregonines" and "gangfisch" for their colouring while still living. We have also attempted to record the various shades in coloured pictures, and in this manner

we have arrived at some conclusions which we consider significant for the characterization of the colouring of the blue coregonine in comparison to the shade of the other races.

Initially, we must emphasize that the basic colouring is subject to great individual variations, that is to say, that there are differences according to the season of the year, differences caused by differences in age and differences directly caused by environmental factors. In July, 1949, which was a warm month I noticed that the "blue coregonines" caught in the Lake near Friedrichshafen were much lighter in colour than those caught near Langenargen during the previous winter and autumn. The intensity of the blackening of the back and in particular the appearance of bluish shades in the greenish-olive basic colour were evidently dependent upon the temperature or the season of the year. The influence of degree of maturity should also be considered in this connection. The "wedding costume" of the coregonines is of a darker shade than their ordinary appearance. This particularly applies to the males, so that experienced spawn fishers can tell the spawners from the milters merely on the basis of the difference in colouring. Generally speaking, the fishermen confirm that "blue coregonines" caught out in the open are darker than those caught close to shore.

More significant than the basic colouring is the blackening or soot-covering of the fins. It is more intensive in the case of blue coregonines than it is in the case of

gangfisch. It must, incidentally, be emphasized that the blackening of the fins is dependent upon the age and it reaches its maximum in mature older milters, and, thus, it can be said to belong to a whole complex of symptoms which we may call "wedding costume and sexual differences".

WAGLER has quite justifiably pointed out that the pigmentation of the "blue coregonine" is more permanent than that of other coregonine races. Perhaps the fact that other coregonines get pale more rapidly, as is the case with the "kilch", is due to the rapid change in temperature to which fish living in great depths are subjected and they are suddenly pulled up into the lukewarm surface water of the Lake in summer, or perhaps a change in colouring is due to the sudden change in pressure.

The shape: The "blue coregonine" is generally fairly slim, but not infrequently more compact specimens are encountered. Mouth is terminal, but not invariably so. WAGLER mentions that he has occasionally also observed subterminal mouths. WAGLER reports the same concerning the gangfisch. He describes the differences as tending to become "fatally small, or even completely blurred when greater quantities of fish are observed. Consequently, it is entirely impossible definitely to identify an individual specimen. A matter which is at least equally problematical is the relative length of the head, which, as is well known, to a great degree depends upon the age. From our own measurements we obtained the following variation tables:

Head Length in Percent of Body Length

14.0	14.5	15.0	15.5	16.0	16.5	17.0	17.5	18.0	18.5
1	--	1	2	5	7	8	8	8	1

These figures correspond quite well to those obtained by WAGLER. Since our measurements also included distinctly large and, on the other hand, quite minute "blue coregonines", our broad variation range which overlaps WAGLER's at both ends is by no means surprising.

There has been a great deal of discussion concerning the eye size of the "blue coregonine" in contrast to that of the "gangfisch", and NUSSLIN even based his specie's name for the "gangfisch" "macrophthalmus" especially on this characteristic. The many sets of figures reported by NUSSLIN, KLUNZINGER, SCHEFFELT and WAGLER make it difficult to form any valid opinion because, as a rule, they contain no data concerning the absolute length of the fish measured. It would be necessary to compare fish of exactly equal size with each other, because young coregonines always intend to have relatively large eyes and old ones relatively small ones. The fact that the mostly young and when older particularly dwarfed "gangfisch" have larger eyes than the more rapidly growing "blue coregonines" is certainly not surprising. The co-efficient of slimness expressed as a relationship of the body length to the maximum circumference has been calculated by SCHEFFELT. We too have examined our material in this respect, but we share WAGLER's opinion that the circumference to a great degree is dependent upon the state of nutrition, maturity and the quantity of reproductive material. We would also like to add that the

bloating of the swimming bladder can seriously affect this measurement so that no great significance should be ascribed to the co-efficient of slimness.

One feature which I must consider entirely unsuitable for the characterization of the "blue coregonine" is the "height of the caudal peduncle", the measurement of which is difficult and unreliable. I have investigated the length of the caudal peduncle instead. It, too, shows few differences. The mean value for the caudal peduncles of the "gangfisch" was 8.06%, i.e., somewhat shorter than that of the "blue coregonines" (8.25%). Certainly no lines separating the 2 species could be drawn on the basis of this characteristic.

The same also applies to the scale count. Variation range of the gangfisch: 62-95; Mean value: 81.2. Blue coregonine: 64-97; Mean value: 83.7. It may be that "gangfisch" does in fact have somewhat larger scales than the "blue coregonine", but a differential diagnosis which would attempt to base itself on this characteristic is entirely impossible. The same also applies to the gill rakers, but it is true that the average number is greater in the case of the "gangfisch" than in the case of the "blue coregonine". The following figures show that the variation graphs overlap in many instances:

	"Gangfisch"	"Blue Coregonine"
According to WAGLER	33-47	33-42
Mean	40.2	36.4
Bone Counts	31-49	29-46
Mean	40.65	36.15

We are thus faced with the problem of deciding our stand in relation to the much disputed "blue coregonine - gangfisch" question. While WAGLER in 1927 came to the conclusion "that absolutely certain species differences hardly exist", he later did express himself in favour of a species separation. We for our part have come to the conclusion that even though genetical differences are present, there is no question of a species specialization. Our view supports KLUNZINGER, who considers the "gangfisch" to be a dwarf form. It could probably be deduced directly from the "weissfelchen" ("white coregonine") while the "blue coregonine" could also be considered to be a pelagic species of the "white coregonine". In the case of the "blue coregonine" a pronounced tendency towards a rapid rate of growth has set in, while the reverse development has taken place in the gangfisch. This can be seen from our rate of growth tabulation.

Concerning the Biology of the "Blue Coregonine"

The characteristic living habits of this fish are much more clearly pronounced than any of the anotomical and morphological differences. Generally it can be stated that blue coregonine swarms avoid the shore and feel at home in the free water regions above great depths, particularly in the Upper Lake where they rise to the surface layers of water during the summer only to disappear to unknown regions for the remainder of the year with the exception of their short spawning period in December. Evidently they inhabit the deeper pelagic zones during their absence. It is unfortunate that we have so little written information concerning the vertical and horizontal migrations of

the "blue coregonine". AUERBACH, MAERKER and SCHMALZ write:

"In spring fishing for "blue coregonines" always starts in the upper part of the Lake between Langenargen and Rorschach, and soon, depending on the yield, it moves into the central parts of the Lake between Friedrichshafen and Romanshorn as well as between Immenstaad, Hagnau and Uttwil, Guttingen. In July and August fishermen usually draw their nets close to the end of the Lake between Meersburg and Munsterlingen. During this period they also visit the so-called "Constance Funnel" and Uberling Lake almost to its very end. From September onwards the fishermen again tend to go further out into the Lake between Hagnau and Immenstaad, and usually the last catches are again made in the upper regions of the Lake."

This phenomenon has for decades mislead fishermen to assume that the "blue coregonines" carry out corresponding migrations in the course of the year, but the question cannot be solved this easily. There are still various decisive factors concerning which we have hardly any knowledge. Where is the spawn? What is the behaviour pattern of the young fish during their first year of life? Do they join these hypothetical migrations? What are the conditions and causes of the formations of swarms? First of all, we should deal with the question of whether in the course of a year certain chemical or perhaps even biological processes do not affect the regime of the Lake and thus could be considered to have some influence upon the coregonine migrations. In this connection we are thinking of currents in Lake Constance which are caused by the fact that the Rhine does not simply come to a complete rest in the Lake as had been

previously assumed, but rather that it causes extensive underwater movements. The currents of Lake Constance have been and continue to be the subject of special research. In addition to this, the vertical currents caused by changes in air temperature and by winds must be considered. During the summer of 1949 I conducted several temperature measurements in the area of the so-called Constance funnel, and simultaneously kept a continuous record of the catches achieved by the fishermen. The summer in question was exceptionally nice, warm and dry and resulted in excellent yields. The fishermen were able to land their quota day after day, and the fish processing co-operatives had a hard time keeping in step with the bountiful supply. Then, there was a sudden short, cold period: Thunderstorms, showers and strong winds. Within 24 hours the temperature of the surface water dropped from 24°C. to 14°C (July 18, 1949) only to rise again to 17.5°C. on the following day, July 19. July 18 was a very poor day for fishing. Subsequently, the catches became normal again. Evidently the blue coregonines had withdrawn from the surface layers of the water where they could be reached with bottleneck-type nets, that is to say, they returned to those strata of the Lake lying at depths of more than 10 m. NUSSLIN already reported that during strong winds the coregonines leave the upper layer of the water and disappear into the depths. The question now arises whether or not thermo conditions of the Lake which vary with the seasons of the year do not, in fact, feign these migrations by simply causing the coregonines to rise from the depths into the upper regions of the water first in the Bay of Bregenz, gradually further west as the year passes. Should this be the case then one would have to assume that vertical and not horizontal migrations are responsible for the

change in the location of the fishing grounds described by AUERBACH and others. I, for my part, have come to think that these 2 views are not necessarily mutually exclusive. The joining together into swarms has been repeatedly observed in the case of many fish populations. By means of marking it has elsewhere been possible to establish that these are also migration swarms. It would, however, be wrong to assume that all the "blue coregonines" of the Lake are equally taking part in these horizontal migrations. Experience has taught us that occasionally good catches can also be landed on the Swiss side of Lake Constance right in the middle of summer at a time when, according to theory, the coregonine swarm should be passing by the Baden or Wurtemberg shore of the Lake. One decisive point, however, one which clearly proves that the fishing grounds deserted by the cortillas of fishing boats have by no means become denuded of fish, is that after the fishermen using so-called bottleneck nets no longer land any catches, sportsmen using the so-called "coregonine machine" continue to land good catches from depths around 30 m. In other words, the coregonines have not migrated horizontally but have simply moved to greater depths. For the time being we will leave the question of whether or not these migrations of coregonines are in the main dependent upon the plankton distribution or whether optical and thermo factors play a part unanswered. We must admit that the biology even of so thoroughly investigated a fish as the "blue coregonine" continues to hold many secrets for us, and it could even be said that some of the problems are only now beginning to appear in their full complexity.

Nutrition

According to AUERBACH, MAERKER and SCHMALZ the stomachs of "blue coregonines" principally contain the following organisms:

Diaphanosoma brachyurum Liévin
Daphnia longispina O. F. Müller
Scapholeberis mucronata O. F. Müller
Bosmina coregoni Mairdd
Alonopsis elongata G. O. Sars
Bythotrephes longimanus F. Leidig
Leptodora kindtii Focke
Heterocope weismanni Imhof
Diaptomus gracilis G. O. Sars
Cyclops strenuus Fischer
Cyclops Leuckarti Claus

This is occasionally supplemented by elements of bottom nutrition such as larvae and pupae, as well as imagoes of chironomidae, frequently fragments of various diptirae, ants, ichweumonidae, mites, yearlings of Perca fluviatilis L., blue coregonine eggs and brown cocoons. According to the authors cited by us some of these elements of nutrition must be designated as "chance nutrition". The most important plankton components which represent the "daily bread" of the blue coregonines are the Daphnia lonispina, Bythotrephes longimanus, Leptodora kindtii, Bosmina coregoni and Heterocope weismanni. On the basis of our own investigation of blue coregonine stomachs, we can affirm the above opinions. Per aps in the past insufficient emphasis has been placed on the fact that the

"blue coregonines" of Lake Constance consume masses of young fish, especially so-called "hürlings", that is to say, young perches. We have counted as many as 30 such fish in a single coregonine stomach, and in this connection we would also like to refer to our Illustration 13 on Page 151 of the German text. While WAGLER in his monograph designates the chironomidae as the food of the "blue coregonine" in the plankton region, we must point out that this group of diptirae evidently is not the preferred food of the "blue coregonine", but rather of the "kilch" and the "white coregonine". We, for our part, have in the course of investigating numerous blue coregonine stomachs only encountered chironomidae remnants on a single occasion.

Growth

On the basis of our own measurements and weighings we have but little to contribute to the problem of the rate of growth of the "blue coregonine". So many authors have investigated the rate of growth of this race for so many years so that as far as figures are concerned, I will simply refer to WAGLER's data in the "Handbuch der Binnenfischerei" ("Manual of Inland Fisheries"), Volume 3, Pages 426-441. Nevertheless I feel obliged to point out that I do not agree with the calculation of growth based upon the scale picture, and I like basing my judgment only on direct measurements together with simultaneous age determination. My reasons for this are reproduced on Page 155, fascicle I. In many instances scales are very difficult to read and evaluate and cause a great variety of errors. Just how doubtful judgments based on them frequently are can be illustrated by the following quotation taken from WAGLER's own work:

"In individual cases it is unfortunately occasionally quite difficult to decide whether a ring should be considered to be a secondary ring or a true winter ring. It is frequently almost impossible to obtain positive, unequivocal evidence either way. The best that can be achieved as a result of a thorough-going comparison of many scales and scale samples is a certain degree of probability. The scale specimens of every single population call for new insight and familiarization..."

In view of this, we have decided not to utilize the numerical data based on LEA, and have constructed our own measurements, which, in the particular case of the "blue coregonine", are only random samplings with the data based on direct measurements conducted by other authors.

	Years									
	1	2	3	4	5	6	7	8	9	10
BRAUN (1923)	-	-	28.0	33.3	34.6	40.0	42.0	-	-	--
MAIER (1910)	-	-	32.0	35.9	39.8	41.6	44.3	45.0	46.0	--
SCHEFFELT (1924)	-	-	31.5	35.0	37.5	39.0	--	--	--	--
HAAKH (1929)	-	-	31.5	34.2	37.3	39.7	43.8	47.3	48.0	--
STEINMANN	-	24.3	27.7	31.3	36.2	40.0	--	45.8	--	52

The fact that these growth figures show such a small measure of agreement is, in our opinion, less due to any differences in the methods of determination, or, as WAGLER believes, erroneous age determinations, but rather to the quite extraordinary "growing apart" of the individuals concerned and the frequently very marked difference in the rate of growth of individual age groups. We obtained our material from various zones of Lake Constance, and in the course of our work we gained the impression that even certain regional differences exist, for

the rate of growth of the "blue coregonine" in Uberling Lake surpasses that of fish of the same race in other zones. Fishermen have known for a long time that particularly large "blue coregonines" are caught in Uberling Lake. My own random samplings indicate that this cannot be explained simply by the greater age of the Uberling "blue coregonines", but also by their actually better rate of growth. This brings to the conditions which may be responsible for differences in the rate of growth in "blue coregonines". As is the case in biology generally, it would be wrong simply to seek "causes". Any process can only be explained by a whole complex of conditions. In view of this, the contraversy between NUMANN-ELSTER on one hand and WAGLER on the other hand appears somewhat strange. The first-named authors believe the amount of nutrition to be the factor determining the rate of growth, while the latter author believes temperature to be the cause. It is certain that both parties are right, and it is equally certain that they both have but an incomplete grasp of the phenomenon. The fact that under otherwise equal conditions an unusual abundance of plankton benefits growth appears obvious. It is equally clear that with an overabundance of plankton the intensity of the metabolism may be significantly influenced by the temperature, but both these factors still in no way explain the "growing apart" of members of one and the same age group in one and the same body of water. A further factor, namely, the population density, must be taken into consideration. Our initial experiments directed at breeding coregonines in hatching ponds have taught us some decisive lessons in this respect: The denser

a population is in a given space, the more obvious the "growing apart" becomes. We know that coregonines live together in swarms almost without interruption, even in small ponds. It is evident that the leaders of the swarm are most successful in obtaining bits of nutrition, in particular, insect nutrition, while those following them are at a disadvantage. This "selection" becomes evermore pronounced, and it is even possible to recognize that individual "fast growers" actually crowd other fish of the same age group away from the food supply. The nervousness and excitement caused by fellow members of the swarm increases with the density of the swarm. Another factor to be taken into consideration is wind, which influences the temperature and plankton stratification in the Lake, and, thus, also the yield of the available pasture and the intensity of the digestive process. The overall curve showing the general course of the water temperature in the Lake throughout the year should also be taken into consideration, for it has been established that as the water temperature affects the maturing of the gonads, which, however, in turn, influences the appetite and brings about the beginning of the fasting period, which is more or less obligatory for all coregonine populations. Then there are additional factors: Changes of habitat in the course of the life of the individual; period of exposure to sunshine, which influences the plankton life, as well as the presence of parasites which varies from one individual to the next. Numerous experiences have shown that inhibition of growth as a result of parasites is a frequent occurence in the life of fishes. Along with these environmental

factors, there are internal, hereditary inclinations and motives which determine the rate of growth of the fish. The whole hormone balance plays an important part, and, in particular, the antagonism between the growth and the sex hormones.

It seems to me that the evaluation of all these factors making up the complex of conditions determining the rate of growth is more important than the sterile "mean values mathematics" which ignores reality and attempts to establish nonexistant "laws of growth", and, at best, ends up by giving some rules concerning the rate of growth of individual races without being able to analyse them in any way. Consequently, let us simply note that the rate of growth of the "blue coregonine" comes closest to that of the "white coregonine", but that the actual growth of individuals and age groups is subject to considerable fluctuations.

Reproduction

The "blue coregonine" of Lake Constance is very clearly a "floating spawner". Spawning grounds are the extensive zones of the open sea, particularly in the quadrilateral formed by Langenargen, Arbon, Uttwil and Hagnau. Having spent considerable periods of time in the depths, large swarms appear directly under the surface of the water in localities where the Lake is particularly deep. Once fertilization is completed, the eggs sink down into the lower zones.

As a rule, spawning activities take place during the first half of December and only last a short period of time. Frequently, even after 10 to 14 days, no "blue coregonine" which has reached spawning maturity can be obtained. In other years

the spawning act may drag out somewhat longer, usually as a result of storms and temperature fluctuations of the surface water. A generally applicable rule is that mature spawning fish can be expected in the fishing grounds as soon as the temperature of the surface water has dropped to 7°C. Initially, not the whole of the spawning swarm is fully mature. From a fisheries management point of view it is important that spawn fishing for artifical breeding purposes should not be started too early, since ignoring this rule would cause great losses due to immature spawn.

The question of whether the "blue coregonine" fasts throughout its spawning period has not been cleared up. WAGLER, who at one time thought it did, was subsequently converted to an opposite view by ELSTER.

There are differences of opinion concerning the age of the fish when it first spawns. The youngest among the males are said to spawn after 3 years, and the youngest spawners after 4 years of life. In this respect, the "blue coregonine" differs from the "gangfisch", both sexes of which mature one to two years earlier.

For us, another interesting aspect of the reproductive process of the "blue coregonine" is the character of the spawn itself. The eggs mostly have a bright, reddish-orange colouring. To judge from published data, the dimensions of the eggs are small. Diameter: 2 - 2.5 mm. The volumetric measurement according to WAGLER is said 73,360 eggs per litre, contrasted to only 55,400 in the case of the gangfisch. Unfortunately, these figures are not accompanied by data concerning the size and age

of the investigated spawners. It appears probable that older "blue coregonines" have larger eggs than younger ones.

On the basis of numerous individual investigations ELSTER established the number of eggs per kilogramme of body weight to be 3,200. It appears that fish spawning for the first time are less fertile, but we are lacking any convincing numerical data.

The duration of the development period to the day of hatching was previously simply given in "day degrees". Extensive investigations have enabled us to establish the inexactitude of this method (AMMANN, STEINMANN, 1948). At the beginning of the hatching period the coregonine larvae are much smaller, much more helpless and much less perfectly organized than towards the end of the hatching period. Coregonine eggs matured in low temperatures result in late and more fully developed larvae than those hatched in higher temperatures. This appears to apply to all races. The incubation period, on the other hand, under otherwise equal conditions, also depends upon the size of the eggs. Large eggs containing large yolks permit a more extended period of embryo development than small eggs with meagre yolks. This probably explains why only 300 day degrees are given as the development period of small "blue coregonine" eggs, while "sand coregonine" eggs are said to take 325 day degrees.

Little is known concerning the subsequent life of coregonine fry under natural conditions. On the basis of observations it has been established that the "blue coregonine" yolk-sack fish rises from the deeper zones into the light surface

water within a short period of time. This coincides with the formation of hatching swarms which probably also remain together later on. In this connection, it may incidentally be mentioned that unfortunately knowledge concerning the biology of the juvenile "blue coregonine" is still quite sketchy. Only in 1950 were Messrs. AUERBACH and MUCKLE (unpublished study, Staad) able to catch coregonine fry hatched in early summer in the surface layers of the Lake's water at a fair distance from shore. The main items of nutrition appear to be nauplii and metanauplii of the Lake Constance copepodae.

The "Gangfisch" ("Wandering Fish")

Since we repeatedly had to refer to the "gangfisch" in the course of our description of the "blue coregonine", we will now limit ourselves to some features which are significant for the characterization of this race.

Colouring

The "gangfisch" is usually greenish to bluish-green in colour, and, according to our experience, it frequently also has a bluish tinge, even though in most cases it can be easily differentiated from a juvenile "blue coregonine" of the same size by its lighter colouring. The basic colour also has brownish and yellow tints which are fairly stable after death, and, thus, enable us easily to tell fish in this state from dead "blue coregonines". The fins of older "gangfisch" have strong soot marks, but this blackish colouring is not very stable. We must nevertheless emphasize it here, for the published literature frequently refers to light or white fins as characteristic features of the "gangfisch". Particularly in the pectoral

fins of dead "gangfisch" yellow to reddish-yellow tints predominate in most cases.

Shape of the Body

It appears significant to me that the true "gangfisch" differs both from the "white coregonine", as well as the "blue coregonine" by the fact that its cross-section more closely approaches a circle, in other words, in less compressed, than that of the former two. The head gives an impression of being pointed. The mouth is subterminal in most cases, but not invariably so. On the basis of a careful comparison of the eye size and taking into consideration that only fish of the same size group must be compared to each other come to the conclusion that the size of the "gangfisch" eye is large. The relevant vario-statistical tables must, however, be interpreted with the necessary degree of caution. The average number of gill raker teeth is somewhat greater than in the case of the "blue coregonine" and particularly greater than the number of gill rakers of the "white coregonine". All remaining measurements as well as the scale count can hardly be considered characteristic.

Living Habits

The main difference between the "gangfisch" on one hand and the "white coregonine" and the "blue coregonine" on the other hand is in the living habits. The primary habitat is the free water region not far away from the submarine deposits of rock closer to shore, but less frequently the open sea which is preferred by the "blue coregonines". The fish can also be encountered at greater depths where it lives together with the "kilch". Its main source of nutrition is plankton, but frequently

insects, in particular chironomidae and corethra, also play a part. Investigations of the stomach of gangfisch coming from deeper waters have shown that occasionally the food intake contains lake bottom mud, together with minute shellfish. The fishing operations for gangfish of varying biotopes were to be carried out throughout the whole year, then even greater variety of nutritional components would most probably result. Unfortunately, fishermen tend to send well-fed specimens from good pastures. I think that it is hardly possible to maintain the designation of the gangfisch as a floating fish living exclusively on plankton. During the spawning period, the main catching period for gangfisch, when it is easier to obtain not fully fed specimens of this coregonines the stomachs investigated by us were almost invariably completely empty. This, I believe, is to a certain extent in contrast to the behaviour of the "blue coregonine" and "white coregonine".

Growth

The growth in Lake Constance is considerably less than that of the "blue coregonine" and the "white coregonine". The data of the various authors show some considerable advergencies.

	Age Groups							
	1	2	3	4	5	6	7	8
SURBECK (1925)	-	-	22.5	26.6	26.5	27.6	29.7	-
HAAKH (1929)	-	-	24.6	26.2	28.1	30.2	31.1	33.5
WAGLER (1937)	-	-	22.6	26.8	29.9	31.1	--	-
STEINMANN (1949)	-22.7		23.7	30.0	32.5	33.4	35.1	-

It should be noted that almost all our measurements were made on spawning fish, that is tosay, fish which had completed the year of their age group, while earlier authors also took

summer catches into consideration. Without again wishing to begin a new discussion concerning the factors affecting the rate of growth, we would merely like to point out 2 factors specifically relating to the growth of the gangfisch: Namely, the frequently considerable density of the swarms and the early maturity of the fish. Both have an inhibiting affect on the growth of the gangfisch of Lake Constance.

Reproduction

The spawning habits are of great significance in the characterization of the "gangfisch". It is a pronounced "early spawner". The testicles of the milters already show considerable development in the second year of the fish's life, and they are fully mature during the third year at the latest. The spawners in isolated cases mature during the second year, the majority in the third year, some in the fourth year. Another characteristic is the long extent of the spawning period. "Gangfisch" in a state of spawning maturity can be obtained on Lake Constance from the middle of November well into the New Year. The eastern regions of the Lake supply spawning mature fish up to the end of January. One should also not omit mention of the fact that at least in individual fishing grounds 5 to 8 year old gangfisch showing a relatively poor growth but considerable growths of spawn are encountered. This proves that the "gangfisch" which started spawning at a very early age pays for this advantage by a reduced rate of growth during subsequent years, and that in this process the predominance of the sex hormones continues to assert itself at a later date. The weights of the gonads which amount to some 20% of the body weight may serve to illustrate this point.

All this shows that the frequently noted large size of the gangfisch eggs is in part due to the fact that the older age groups among the spawning fish are particularly well represented among the producers of spawn material used in artificial hatcheries. The "gangfisch" also clearly differs from the "blue coregonine" in that they prefer entirely different types of spawning grounds. Like the "white coregonines" they a spawn in shallow water close to shore and also seem to like the vicinity of the mouths of streams and the so-called""Lake Rhine" between Lake Constance and the lower Lake. Near Paradies-Gottlieben-Ermatingen gangfisch spawning ground have been known for many generations. As has already been mentioned, the eggs are relatively large. One litre contains approximately 55,000 of them. Under otherwise equal conditions the incubation period is somewhat longer than that of the blue coregonine. The larvae have a darker pigmentation, and their development is more advanced than that of "blue coregonine" larvae. Early gangfisch eggs caught for artificial breeding should be kept in water having a low temperature. In its other spawning habits the gangfisch is fairly similar to the "white coregonine". It appears to be a dwarfed tribe of the "white coregonine" type, a coregonine with a reduced growth potency, in other words, a hereditary dwarf form differing from the primigenius by its early maturity and corresponding poorer growth.

The "Sandfelchen" ("Sand Coregonine")

The "sand coregonine" has become fairly rare in Lake Constance. Perhaps this is also due to the fact that it is not the object of many fishing operations. Fishing operations using bottleneck-type nets has placed more emphasis on the "blue coregonines

and the fixed nets used close to shore and in shallow regions of the Lake are less suitable for catching this larger race. In spite of these factors, we have gained the impression that the sand coregonine has, in fact, become rarer. The best chance of catching this fish is in the lower Lake where so-called draw nets are used, and where it may be caught together with the "white coregonine" from which some fishermen are unable to tell it.

Colouring

WAGLER is of the opinion that the "large bottom renke" has a colouring which comes closest to that of the "blue coregonine", and that some of its external characteristics can be told from those of the latter fish only with difficulty. According to WAGLER there is some soot colouring of the fins, but it is less highly developed than in the case of the "blue coregonine". We, for our part, have seen freshly caught sand coregonines with extremely dark ventral fins. This again confirms that judgments concerning questions of colouring can only be made on the basis of fresh or, wherever possible, living material.

Shape

When viewed from the side, the shape of the "sand coregonine" is invariably more compact than that of the "white coregonine" and particularly the "blue coregonine". The body appears more compressed than that of the "gangfisch". In the case of older specimens, the back starts rising steeply just behind the head (see Illustration 63). The fact that the snout is slightly shorter than that of the other coregonines

of Lake Constance, this is also somewhat reflected in the head length index, but only to a limited extent.

Head Length Index Mean Values

"Gangfisch"	18.2%
"Kilch"	18.1%
"Blue Coregonine"	16.9%
"Sand Coregonine"	16.5%

Since the "sand coregonine" are, on the average, caught in considerably larger specimens than the other coregonines, some of its mean values show somewhat different proportions.

The mouth is always clearly sub-terminal. I consider this typical shape of the nose of the sand coregonine to be one of the most characteristic features of the race. On the Lower Lake it enables us to tell "sand coregonines" from "white coregonines" at a glance. It is noteworthy that WAGLER, who did not differentiate between the "white coregonine" of Lower Lake and the "sand coregonine", has written about the "sand coregonine of the Lower Lake approaching the "blue coregonine" for the terminal position of the mouth could frequently be observed". This part of WAGLER'S study, compiled in 1937, clearly shows that the two types studied by WAGLER were the ecotype literalis as well as the ecotype primigenius.

In most cases the caudal peduncle of the "sand coregonine" appears to be somewhat shorter than that of the other coregonines of the Lake Constance region, but our measurements have been unable to confirm this, and the mean value does not differ from that of the other forms. Gill rakers are particularly worth noting, for they are more powerful and less densely spaced

and shorter than those of the floating coregonine. The gill raker variation range of the fishes examined by us was 18 - 27 with a mean value of 22.3. This corresponds fairly well with WAGLER's figures. Formed and deformed gill rakers are not at all rare, particularly in older specimens.

"Sand coregonines" are mostly found near the shore regions. When pasturing their swarms are not too large and frequently they are also counted singly on submarine rock deposits close to shore where they eat tiny fish, snails, worms, insects frequently mixed with vegetable detritus and mineral, mud and slime. The contents of their intestines can be almost black in colouring. There are also individuals who occasionally live on crustation plankton.

The rate of growth of the sand coregonine is considerably better than that of the other coregonines in the Lake. This may be due to environmental factors -- abundant nutrition, warm water near the shore region and slight density of swarms. To this should be added such internal factors as an inherited growth potency. Sand coregonines are late spawners, who, as far as we can judge, achieve maturity only during the fourth year of their life and occasionally even later. It is very difficult to encounter younger coregonines in the spawning grounds. When this does happen occasionally, then the fish in question appear to be immature predators who have joined the spawning swarms in order to feed on the eggs. Already SURBECK (l.c.) found coregonine eggs in the stomachs of "sand coregonines". We must, by the way, emphasize the great difference which may exist in the rate of growth, and even in SURBECK's time he was

able to report about a seven-year old "sand coregonine" measuring but 31 cm in length which he was able to compare to 4 and 5-year old specimens measuring more than 40 cm. Obviously, this great difference in the rate of growth, which we can fully confirm on the basis of our own investigations, can be ascribed to the varying living conditions of this fish of solitary living habits. We have encountered the following extremes:

3-year olds: 24.1 to 38.9 cm

4-year olds: 23.3 to 42.5 cm

5-year olds: 34.0 to 50.0 cm

Another very conspicuous fact is that sand coregonines have been observed to be fully active spawners even at such high ages as 8, 10 and even more years. We have been able to witness this repeatedly near Ermatingen on the Lower Lake. In other races senile degeneration has already set in at this age. It appears that on the whole these fish have a longer life span than the members of other races. Probably the "white coregonine" approaches them most closely. We have seen individual old specimens of the latter in full spawning maturity.

The "sand coregonine" is a late-maturing, rapidly growing variety which is based on the primigenius type, and still is closely related to it, the morphological differences being the terminal position of the mouth and the greater distance between the gill raker teeth. Biologically, they are marked by their adoption to closer shore waters and their selection of the edge of the water as spawning grounds.

THE "KILCH"

The kilch can be found in the Upper Lake as well as in the Lower Lake at depths of 20 and more metres. Its habitats change in the course of the year. More "kilch" are caught on the German side of the Lake than on the Swiss side. This may be due to the application of different fishing methods. Most of the typical "kilch" I investigated came from the Berligen-Steckborn zone on the Lower Lake, the area formed by the "Constant Funnel" - Meersburg - Mainau, further from Romanshorn, langenargen and Lindau. In July, 1949, they had an opportunity to examine several kilchs coming from depths of approximately 100 m.

None of the coregonines of Lake Constance can be diagnosed so easily and definitely as the kilch.

Colouring

WAGLER states: "It is always fallow, more brownish in colouring". This applies to the dead fish, but not to the living. We have repeatedly examined living or very freshly caught "kilch", the colouring of which was vivacious. Their backs had a pronounced dark tint, and their fins had soot marks. I noted the yellowish-red pectoral fins which reminded me of the "white coregonine" and the "gangfisch". Particularly in the case of the "kilch", the tips of the pectoral and ventral fins have strong soot markings, and they are usually conspiciously pointed. Probably the sudden change in temperature and pressure to which fish raised from great depths are subjected causes a rapid dying off of the chromatophores and the sudden decolouration. I am reinforced in this assumption

by the behaviour of "kilch" caught in shallow water of the Lower Lake in winter. These fish maintain their colouring much longer than the "summer kilch" originating from greater depths of the Upper Lake.

Shape

"Kilch" which are not suffering from tympanitis are slim. The length of the head corresponds with that of "sand coregonines" and "gangfisch" of similar size. If the "kilch" in WAGLER's tables appear to have relatively large heads, then this is due to the fact that the author mostly measured small specimens, which had correspondingly large heads. If we compare "sand coregonines" and "kilch" of the same sized categories, then on the basis of our material the head length indicies of the two fish are very similar.

Mean of 18 "sand coregonines" measuring 28 to 32 cm in length: Head Length index - 17%

Mean of 19 "kilch" measuring 28 to 32 cm in length: Head Length index - 17.8%

The shape of the head is close to that of the sand coregonine, that is to say, the forward part of the snout is somewhat bent, and the mouth is clearly sub-terminal. When fish of the same size are compared, the relatively large size of the eye of the kilch becomes clearly evident. This can also be seen from the following figures compiled by us:

Mean of 18 "sand coregonines" measuring 28-32 cm in length: Eye size in percent of body length - 3.8%

Mean of 19 "kilch" measuring 28-32 cm in length: Eye size in percent of body length - 4.1%

The scales of the "kilch" are, if anything, somewhat larger than those of the other races. The mean value as determined by us was 76.6 in contrast to 82 reported by WAGLER. The extremes were: 65 and 87. Naturally, the figures obtained for the other races variously overlap those mentioned here. Consequently, this feature can also not be used for purposes of diagnostic differentiation, but only as an aid towards the overall characterization.

The pectoral fin of the "kilch" was already considered relatively long by FATIO. This is also evident from WAGLER's figures: Mean value for the kilch of Lake Constance 14.2%, extremes 12.5 and 16.5%. This difference appeared even more markedly in our own investigations. This is evidently due to the fact that the material examined by us contained a considerable number of larger "kilch". The overall mean value as determined by us amounts to 4.8%. In the case of five-year old and older "kilch", it even reaches a mean value of 15.4 and a maximum of 17.5%. This confirms the experience that the pectoral fins of older fish show a particularly good rate of growth. I also noted that the first fin-rays formed a sharp point which was very strongly soot-covered in the case of old specimens.

The gill rakers are very characteristic, having a short and broad appearance, and conspicuously few secondary thorns. (see Illustration 11, Page 143 of the German text).

Growth

WAGLER's figures, which were at my disposal, and my own measurements and age determinations have contributed little towards a clarification of the problem of the "kilch"

growth. I consider WAGLER's figures based on the growth of scales particularly doubtful because age determination based on scales is particularly uncertain in the case of the "kilch". The fact that this inhabitant of the depths maintains fairly uniform living habits throughout the years, and the fact that its spawning period lasts several months, frequently make the year-marks on the scales indistinct. "Kilch" scales can occasionally bring one to despondency. Now if even the determination of the number of years is doubtful, how much more difficult is it to calculate the rate of growth on the basis of the scale rings. We have handled "kilch" in a great variety of sizes, and have gained the impression that this fish, just like the "sand coregonine", is subject to considerable growth fluctuations. Perhaps this may be due to the varying abundance of favourable pasture grounds in the depths. Our dredging investigations conducted in other lakes have shown that conditions on the bottom of a lake are by no means uniform, and that the submarine pastures abounding in organisms alternate with their sterile zones. The "kilch" evidently migrates, and in the course of its travel, it more or less depends on luck to find pasture grounds. Temperature hardly influences its rate of growth because temperature fluctuations within its habitat are only very slight throughout the year.

Mean length of age grounds as determined by WAGLER according to scales in comparison with our own direct measurements:

	Age Groups						
	1	2	3	4	5	6	7
WAGLER	9.3	16.7	22.0	26.3	29.4	31.8	35.5
STEINMANN			24.7	25.1	28.4	32.5	38.1

Here again the extreme values are more instructive than the mean values:

Age Groups				
3	4	5	6	7
21.0-31.8	21.0-30.0	23.5-39.5	26.6-41.0	32.5-41.0

The material refers to 98 specimens.

It is evident from our figures that the "kilch" certainly is not deserving of its reputation as a fish having a poor rate of growth, and that at least individual specimens show very good growth. We could be sure that we actually were examining "kilch" and not perhaps "sand coregonines" because most of our studies took place during the spawning period, and, as is well known, the spawning grounds and seasons of the "kilch" and the "sand coregonine" are entirely different.

Reproduction

Like other coregonines living in the depths, the "kilch" has an extended spawning period. I had an opportunity to become convinced of this fact in 1949 when fullymmature male and female "kilchs" could be caught in "Constance Funnel" near Staad, as early as during the first half of July. On the other hand, it is still possible to get "kilch" eggs as late as November, and if fishermen would not be preoccupied with "sand coregonines", "gangfisch" and "blue coregonines" during this season of the year, they could probably catch individual

"kilch" as late as New Year's Eve, as they are able to catch "albeli" in Lake Lucerne. We still know practically nothing concerning the spawning grounds and details of the laying of the eggs and their development. This is due to the fact that the reproductive process of the "kilch" takes place in the dark depths of the Lake. We also don't know anything concerning the initial nourishment of the young "kilch" fry. Further investigations concerning these matters are still necessary.

Illustrations on Page 489 of the German text:

59: Lake Constance: "Weissfelchen" ("White Coregonine").

60: Lake Constance: "Kilch".

61: Lake Constance: "Blaufelchen" ("Blue Coregonine").

62: Lake Constance: "Gangfisch" ("Wandering Fish").

63: Lake Constance: "Sandfelchen" ("Sand Coregonine").

Nomenclature

"Weissfelchen":	Coregonus lavaretus L. nat. bodanensis, ecotype primigenius,
"Sandfelchen":	Coregonus lavaretus L. nat. bodanensis, ecotype litoralis,
"Blaufelchen":	Coregonus lavaretus L. nat. bodanensis, ecotype pelagicus,
"Gangfisch":	Coregonus lavaretus L. nat. bodanensis, ecotype nanus,
"Kilch":	Coregonus lavaretus L. nat. bodanensis, ecotype profundus.

Lake Constance

	No.	Circumference	Head Length	Eye Diameter	Caudal Peduncle
"Weissfelchen"	191	44-64 Mean 51.3%	15.5-24.5 Mean 17.91%	3.0-5.1 Mean 4.04%	6.5-11.5 Mean 8.27%
"Sandfelchen"	152	44.5-64 Mean 54.5%	14.5-24.5 Mean 17.22%	2.8-5.0 Mean 3.57%	5.5-9.5 Mean 7.78%
"Blaufelchen"	41	45-54.5 Mean 49.35%	14-18.5 Mean 16.93%	2.9-4.4 Mean 3.58%	7-10 Mean 8.25%
"Gangfisch"	245	43-62 Mean 51.7%	15-22.5 Mean 18.10%	3.2-5.2 Mean 4.19%	3.5-11.5 Mean 8.06%
"Kilch"	65	45-64.5 Mean 55.6%	16.5-21 Mean 18.03%	3.4-5.1 Mean 4.39%	5.5-9.5 Mean 7.95%

Lake Constance (Cont'd)

	No.	Length of Pectoral Fin	Scale Count	Gill Raker Count
"Weissfelchen"	191	10.5-17, Mean 13.4%	70-99, Mean 81.4	24-39, Mean 33.35
"Sandfelchen"	152	11-19, Mean 13.91%	71-99, Mean 85.65	18-27, Mean 22.35
"Blaufelchen"	41	11-16.5, Mean 13.01%	64-97, Mean 83.7	29-46, Mean 36.15
"Gangfisch"	245	11-19, Mean 13.63%	62-91, Mean 81.2	31-49, Mean 40.65
"Kilch"	65	12.5-17.5, Mean 14.83%	65-87, Mean 76.6	14-25, Mean 19.97

MONOGRAPH OF THE SWISS COREGONINES

A Contribution to the Problem on the Formation of New Species

By Paul STEINMANN, Aarau

Received on June 15, 1950

U. THE INSUBRIAN LAKES

(Lago Ceresio - Lake Lugano, Lago de Verbano - Langen Lake or Lake Maggiore)

There are no primary occurrences of coregonines south of the Alps. Their introduction in the waters of this region has proven to be an extremely successful experiment, and today the coregonine stocks are considered a very valuable enhancement of the regions concerned. The coregonines have even become a fish of first-class economic significance in this region. Italian ichthyologists, particularly Pietro PAVESI and G. ERSANA, later Rina MONTI and her students, have taken a lively interest in this large scale experiment and have supervised the development from the very beginning. A humber of valuable studies concerning this matter are available. For us, these findings lead to a series of significant conclusions, which make it appear desirable to include the coregonines of the southern lakes in our considerations.

Historical

The first introductions took place in Lake Garda and in Lake Maggiore in 1880. They were continued with interuptions until 1896. Subsequently, the supply of local fry was sufficient to produce enough eggs for the continued planned management of the Lakes.

Lake Lugano obtained it first stocks in 1896. Subsequently, it was in the main dependent on breeding stock from Lake Como. On the basis of material available to me, I have attempted to make the following compilations of nations and ecotypes from Northern Switzerland which were originally introduced into these Lakes:

1. The "blue coregonine" of Lake Constance
2. The "sand coregonine" of Lake Constance

Terese STOLZ's study, written in 1929, does refer to "weissfelchen" ("white coregonines"), but the author adds the scientific name, "Coregonus schinzii Fatio sub-species helveticus var. bodamensis". Evidently, this refers to the Coregonus lavaretus L. nat. bodanensis, ecotype primigenius. Terese STOLZ investigated five coregonines from Northern Switzerland which were collected during the epoch of the main experiment conducted by PAVESI and handed over to the Museum of Pavia University. Four of them were reported to originate from "Lago di Costanza" (Lake Constance) (1883, 1893 and 1894) is designated "weissfelchen" ("white coregonine") and was included in the Pavia collection in 1893.

3. The Zuger Lake "Palchen"

The files also contain a mention of Zuger Lake as one of the places from which fry was obtained. The fish in question, the eggs of which were at that time brought over in Gotthard's Pass, figures under the name of Coregonus schinzii helveticus Fation var. zugensis. According to our nomenclature, it would have to be called Coregonus lavaretus L. nat rïusensis ecotype primigenius.

While it is impossible to prove it, nevertheless it appears very probable the main introductions of fry from 1883 to 1896 came from the hatcheries of the "Lower Lake". The term "weissfelchen" ("white coregonine") which repeatedly appears was not current on the Upper Lake, but only on the Lower Lake, when the fishermen still differentiated the "weissfelchen" ("white coregonine") from the "sandfelchen" ("sand coregonine"). The latter was found less frequently and only larger specimens of it were caught. Thus, there are good reasons to assume that the "white coregonine" (Primigenius) was transferred from Lake Constance to the southern lakes along with the "blue coregonine". The "balchen" of ZugerLLake, which at that time supplied stocking material for the lakes of the Tessin, according to our opinion, also belongs to the Primigenius group. Unfortunately, I was unable to ascertain the numerical relationships of the various fishes introduced into these lakes.

The Pressent Status of the Coregonine Problem in the Southern Lakes

There now arises the question of what has become of the numerous "blue coregonine" and "white coregonine" fry which were brought to the insubrian lakes from Northern Switzerland in the course of the seoond half of the last century. Have they become a uniform population in this melting pot? Are there today certain morphological or ecological differences between the populations of the individual insubrian lakes? Has there been any development of characteristics which would differentiate present-day stocks of the southern lakes from those of the north? Do the special climatic conditions prevailing in the south perhaps in some way influence the rate of growth, or perhaps the reproductive processes of the fish? If they do,

are the changes merely modifications, or is it already possible to determine genotypical changes? The most insignificant investigations capable of aiding the solution of these questions have been conducted by Rina MONTI, together with her co-workers. We, for our part, also attempted to clarify the most important questions on the basis of coregonine material from Lake Maggiore and Lake Lugano, and this initial report is a representation of the presently existing fundamental conditions.

T. STOLL (l.c.), unfortunately, recorded the physical characteristics of the objects investigated by her according to a method which is different to the one usually used by us. She principally concentrated her attention on five features, which have received little or no attention in our own tables:

1. The length of the body (altezza del capo) - Body length without tail fin;
2. The height of the head (altezza del capo);
3. Predorsal interval (spazio predorsale) - the distance from the point of the head to the origin of the dorsal fin;
4. Length of maxillary (lunghezza della mascella);
5. Shape of throat (gola) - the numerical relationship between the length and the width of the inner maxillary field (c.f. Illustrations 10, 12, fascicle I, Page 142 of the German Test).

Unfortunately, our Italian colleague measured the body length differently than we did. By "lunghezza del corpo", distance from the point of the snout to the rear-most scale on the tail fin, is meant, and not the "lunghezza totale", a measurement which also includes the tail fin. We are, without

further ado, prepared to recognize certain advantages inherent in this method, particularly in the case of specimens which have disproportionately large tail fins (acromegalia). On the other hand, the individual scale pattern on the pectoral fin varies very considerably, particularly in the case of the coregonines. Not infrequently the scales overlap the bases of the fins to a considerable extent. This is quite changeable within one and the same population. In view of this, the body length is less satisfactory as a reference value than the total length. In any case, we were unable to do a great deal with the measurements included in STOLZ's study, since we were lacking a basis for comparison. A conversion of the total length into body length would also not be considered, because, as has already been mentioned, the size of the tail fins varied too much. Only the data concerning the number of gill rakers enable us to a certain extent to compare STOLZ's figures with ours. In the following section we first attempt such a comparison on the basis of the approximately fifty coregonines, which we were able to measure and investigate ourselves, and a few measurements which we were able to ascertain on the basis of old museum specimens put at our disposal.

Our tables and the graphic representations show that the coregonines of Lake Maggiore represent a fairly uniform population, even though they were caught in various locations at different times and with variety of fishing devices. There is no indication whatever of a decomposition into a Litoralis and a Pelagicus type. On the whole, the fish are of average proportions. The variation range in the case of most of the

features which we were able to record statistically is smaller than in Lake Constance. There arises the question of whether the extreme types of the "floating coregonines" (Lake Constance blue coregonine") and the snub-nosed, coarse and unwieldy "sand coregonine" of the Literalis group can be considered as exterminated or extinct, or whether their blood has become mingled in the average forms, which characterize the Lake at present. In this connection, it should be stated that even the starting materials from Lake Constance and Zuger Lake were variable and that the whole complex of coregonine tribes from the southern types originate cannot be considered as a clearly defined species, but merely as a mixture of various genotypes, a mixture which was at least as varied as the present-day coregonines of the southern lakes. Probably, if we searched enough, Lake Maggiore would also yield fish with pronounced "floating coregonine" characteristics, whose body dimensions and gill raker structures would approach those of the "blue coregonine" type, and, on the other hand, also specimens which more closely approach the Literalis type. Lake Maggiore, probably also the other insubrian lakes, are in this respect no different than most of the lakes of Northern Switzerland; all of them are inhabited by a varied mixture of coregonine types. Sooner or later a specialization will take place as a result of certain partial populations developing specific morphological and ecological characteristics. If this development takes place in isolation, that is to say, if the tribes in question no longer cross breed with those of other ecotypes, then specializations, which will present future authors with all sorts of puzzles, will take place. Today I am not in the position to regard such starting specializations as being originally caused

by environmental factors and only later becoming heriditary. The availability of varied genotypes is, without doubt, very great, and natural selection eliminates what is useless in order to foster the development of suitable types.

The fact that the rate of growth in the southern lakes is somewhat better than in the northern ones may be connected with the fact that the winter is shorter and less severe so that the winter fasting period is less extensive than in the lakes of Northern Switzerland. In addition to this, it may also well be that the high summer temperatures cause the deeper layers of water in the insubrian lakes to become warmer, and probably also to develop more plentiful plankton supplies than is possible north of the Alps.

Let us assume that the start of sexual maturity depends upon the temperature, that is to say, that the reaction norm of a given coregonine type caused it to achieve spawning maturity at, let us say, 7° C. It is evident that under these circumstances the coregonine calendar in the south would differ somewhat from that in effect in the north. It is, however, by no means necessary for such changes to be connected with any heriditary factors. The question of whether the reaction norms of different coregonine populations of one and the same Lake differ is another problem. It is by all means possible, yes, even probable, that here again we are faced with the effects of an environmental, as well as a heriditary, component.

As far as nutrition is concerned, it will on the whole not differ too much from that of the northern lakes. The investigations of stomach contents conducted by us showed that

The coregonines caught in Lake Maggiore, had, in addition to plankton, also consumed considerable amounts of insect larvae and pupae. In addition to a food intake of flying insects, which may have reached the surface of the water from the shore, we were also able to find a particularly great number of mosquito larvae, which the fish appeared to have brought up from the bottom. Thus, the southern coregonines proved themselves by no means particularly rigid from an ecological point of view, and in this respect too, they can probably be considered as intermediate forms between the "floating coregonines" and the "bottom coregonines".

According to STOLZ, we must assume that the individual Lombardy lowland lakes are already beginning to show certain differences in coregonine types. Even though the material studied by Italian researchers to date is not very extensive, it does allow certain conclusions. Unfortunately, we do not know whether these differences are the result of unequal original types dating back to the period of initial introduction, or whether they are modifications or the results of a genotypically founded differentiation. It would be well worthwhile thoroughly to re-examine the whole problem once more.

Some Data To Aid In the Characterization of Coregonines Presently Inhabiting the Lakes of the Tessin

The coregonines, which I handled -- a total of some 50 specimens -- were neither particularly slim nor particularly compact. This also finds its expression in the co-efficient of slimness:

Circumference expressed in terms of percent of body length: 44.5-54.0, mean 49.3.

Had we carried out our investigations during the spawning period of the fish, then different figures would have, of course, resulted. In comparison with the typical "floating coregonines" of other lakes, the fish tend to be rather compact. This may also be due to the fact that we did not obtain any small coregonines.

The head length index also does not call for any special comment: 15.5-19, Mean 17.2.

These figures easily fit the picture of the Primigenius. The same applies to the length of the caudal peduncle: 7-11, Mean 9 as well as eye diameter: 2.5-4.4, mean 3.65.

Here again it was very evident that the larger, older specimens had smaller eyes than the younger, smaller ones.

The scale count of the coregonines of the Tessin also corresponds to that of the Primigenius of northern Switzerland: 77-93, mean 85.

The same is the case with the gill raker count on the first arch: 26-37, mean 31.7.

I would not like to attach too great a value to the result of a single investigation. It is possible that the variation range and mean values of other swarms in the same Lake may take on a different appearance. Nevertheless, we can safely state the following:

The present-day coregonines of the Tessin by no means belong to the ecotype pelagicus, and even to a lesser extent to the litoralis group. They stear a middle course. This may be

connected with the fact that the vast majority of the original forms were "white coregonines" of the Lower Lake in Lake Constance and the "balchen" of Zuger Lake; the "blue coregonine blood" was evidently overwhelmed.

The rate of growth is definitely better than that of their relatives from Northern Switzerland. R. MONTI already recognized this:

"L'accrescimento nei nostri laghi e maggiore di quelle di coregoni d'oltra Alpi..."

Our own rate of growth curve is not too soundly based, since we were in the main confronted with three and four-year old coregonines, and only exceptionally two and five-year old ones. In spite of this, we will reproduce the measurements here:

2 year olds.....31.5-35 cm
3 year olds.....32.2-36 cm
4 year olds.....40.5-42 cm
5 year olds.....41 -44 cm

An isolated, 47-cm long animal appears to have been 6 years old. I have never seen any older specimens.

From Lake Lugano (Ponte Tresa Basin) I received several coregonines almost every day throughout the summer months, and I have noted their individual features. They hardly differ from the coregonines of Lake Maggiore. Generally speaking, coregonines are considered fairly rare in Lake Lugano, but not a great deal of energy is expended in fishing for them, since other species of fish are preferred by the fishermen.

The apawning habits of the coregonines of the Tessin are, on the whole, similar to those of their ancestors. Large, wandering

swarms can be observed as early as in autumn. They like to seek the vicinity of the mouths of rivers, and, in the course of moving there, considerable numbers of them are caught and used for artificial hatching. The spawn is laid in November and December.

The artificial breeding of coregonine fry is flourishing in Lake Maggiore, but coregonine spawn fishing operations are also diligently conducted in the neighbouring lakes of Italy, particularly in Lake Como. This has, without doubt, contributed a great deal to these coregonines spreading over ever-extensive areas in so short a period of time.

V. A GLANCE AT THE COREGONINE WATERS OF THE REMAINING ALPINE REGIONS

I could be accused of being one-sided if I were to limit my monography entirely to bodies of water located within Swiss territory. The problem of the formation of species with which we are occupied can in the final analysis only be brought closer to a satisfactory solution by an all-encompassing synthesis of the whole observation material, including the research results of foreign colleagues in this field. The difficulty encountered in this connection is due to the fact that practically every researcher uses his own criterii and methods of measurement in approaching his material, so that the figures supplied by him cannot be used for comparisons without being subject to further examination.

Consequently, I decided to include some foreign materials in my comparisons. I also briefly surveyed museums in Switzerland, as well as the collections of the museums of Vienna, in order to obtain an overall view. My study and collection trips in 1948 and

1950 were particularly fruitful, for they enabled me to examine fresh material from the following Lakes:

Lac due Bourget
Alp Lake near Immenstadt
Koche Lake
Ammer Lake
Lake Chiem
Atter Lake
Lake Traun

In addition to this, preserved materials from Wörthe Lake and Hallstädter Lake.

Introductory remark: My investigations dealing with bodies of water outside of Switzerland were only informatory in character. Nothing was further from my mind than a revision of the studies compiled by WAGLER and others. To do this, I would have required much more extensive material than that which was at my disposal. What I was concerned with were some measurement results in order to examine criterii which had been ignored by previous authors, as well as the very desirable opportunity to examine freshly-caught coregonines for their colouring. In the following section, I would like to publish some details which, in my opinion, support my concept of the genesis of the coregonine race.

Ammer Lake

I encountered the frequently-discussed "kilch" of Ammer Lake in 13 completely fresh, mature and immature specimens ranging in size from 20 to 27 cm, in weight from 75 to 183 g. A certain similarity to the "kilch" of Lake Constance certainly exists, for

both belong to the "ecotype profundus". There were, however, also considerable differences in details, which, to my mind, appear to indicate autochtonous origin of the two ecotypes. Completely fresh "kilch" from Lake Constance are quite dark, their dorsal and tail fins were uniformly black in colour. The Ammer Lake kilch had a light olive basic colour. The dorsal fin was yellow and/in the case of all specimens, it had a very conspicuous jet-black point, the like of which I have yet to see in the case of any other coregonine type. The other fins also were intensively soot-marked at the points. The iris was of a reddish-brassy colour I have never previously observed in the case of kilch. I conducted my measurements with my usual methods. They are not too divergent from the variation range established by WAGLER's measurements:

	According to WAGLER	Mean Values	According to STEINMANN
Head Length	18.2-21.6	19.3	17 -19
Eye Size	4.2- 6.1	5	4.5- 5.25
Pectoral Fin Length	12 -16.5	14.1	13.5-17
Scale County	73 -89	81.9	65 -75
Gill Raker Teeth on first gill arc	19 28	23.1	18 -24

I refrain from calculating any mean values, since the material is not sufficiently extensive for this purpose, but it nevertheless is noticeable that my minimum values were, in part, lower and my maximum values higher than those determined by WAGLER. This indicates that WAGLER with his approximately 100 measurements -- in part, the data is also based only on some 50 measurements -- still did not cover the whole of the variation

range of the "kilch" of Ammer Lake. Its means values would probably still be subject to certain changes if the statistics were based on a greater amount of material. The difficulties which the systematician encounters in connection with the kilch of Ammer Lake will be discussed elsewhere (Page 108 of the German text).

Unfortunately, I have to date not been able to obtain any material corresponding to the other two coregonines of Ammer Lake, which WAGLER calls "gangfisch" ("wandering fish") and "sandfelchen" ("sand coregonine"). The data supplied by WAGLER is very sparse. In the literature available to me I was unable to find any mention of the "sand coregonine" of Ammer Lake, even though I was vitally interested in this fish, which appears the probable ancestor of the Ammer Lake kilch. WAGLER diagnosed the "gangfisch" of Ammer Lake on the basis of some 100 specimens. This fish has smaller eyes (mean value 4.2 as against 5 in the case of the "kilch") and has a shorter head (18.1 as compared to 19.3 in the case of the "kilch"). As I have repeatedly explained, I, for my part, do not assign a great deal of value from a diagnostic point of view to the head length index and the eye size. Nevertheless, I would like to point out that it is just in these dimensions that my material shows certain deviations from that studied by WAGLER. I would not be surprised if more extensive statistical investigations, which have yet to be conducted, would somewhat equalize the differences presently separating the "gangfisch" from the "kilch".

As far as the gill rakers are concerned, extreme values according to WAGLER just touch, for the maximum figure given for "kilch" is just under the minimum figure for "gangfisch". Had

the "sandfelchen" ("sand coregonine") been available for inclusion in the table, then very probably a considerable overlap would have resulted, and the continuous variation range, which is so characteristic of other lakes, would also have become apparent in the case of Ammer Lake.

As far as I can testify on the basis of my own investigations, the detailed structure of the gill raker teeth of the Ammer Lake kilch differs considerably from the corresponding formations of the "kilch". The assumption that the Ammer Lake represents an autochtonous type profundus of this nation, which is part of the Ammer Lake coregonines, lies close at hand.

Kochel Lake

I examined 15 coregonines ("renken") of Kochel Lake. According to WAGLER, they should have been "gangfisch" or "sand coregonines" occurring in this Lake. In his studies, WAGLER says nothing whatsoever concerning the latter. The former, according to extracts from the tables compiled in 1937, can by no means be compared with the "gangfisch" of Lake Constance. Let us just compare the corresponding gill raker count figures: Lake Constance: 33-47, mean: 40.2, Kochel Lake: 26-37, mean: 32.7. My figures correspond quite reasonably to those ascertained by WAGLER. The pectoral fins were larger, presumably because I was mostly handling 4-year old and older specimens. WAGLER's statistics cover some 80 specimens. My minimum scale count is lower than WAGLER's. My maximum eye size index is somewhat higher than WAGLER's maximum. The presently available characterization on the basis of statistical figures is insufficient to consider the "renden" of Kochel Lake as a "gangfisch" within the

Lake Constance meaning of this word. In my opinion, at present this type should be considered as belonging to the "ecotype primigenius" and it certainly is closer to the "white coregonine" of Lake Constance than to the "gangfisch" of that Lake.

Lake Chiem

I devoted my very special attention to this Lake. Previously, WAGLER had reported "blue coregonines", "gangfisch" and "sand coregonines" from this Lake. The occurrence of a "kilch" was first disputed, but subsequently (1950) admitted in line with earlier authors believed to have recognized characteristic "kilch" among certain tribes of the coregonines of Lake Chiem.

I, for my part, obtained considerable numbers of "renken" from Lake Chiem as early as 1947/1948 and more recently in 1950, and I, thus, have at my disposal more measurements than in the case of coregonines of other foreign lakes.

As far as the "sand coregonine" is concerned, it is not mentioned anywhere in WAGLER's tables. They merely contain "blue coregonines" and "gangfisch". Originally, WAGLER assumed that at present Lake Chiem was populated by a "mixture-type" lying between the "gangfisch" and the "kilch", and that this fish, its appearance and biology, had still preserved the character of the "gangfisch",but that its gill raker apparatus indicated the presence of "kilch" blood. According to WAGLER, the "blue coregonine" of Lake Chiem also really does not belong among the "blue coregonines" because of its particularly low gill raker count.. In view of this, I looked forward to my

experiences with Lake Chiem coregonines with great interest.

If WAGLER in 1950 stated that after the matter had been duly explained to them, the fishermen of LakeCChiem were now in a position to differentiate between the different "species" without difficulty, then I counted exactly the opposite, namely that both the Lake supervisor, as well as the fishermen present, were most uncertain in their specifications. I found this understandable. In fact, there was a great variety of characteristics, both from the point of view of shape, as well as colouring: Bluish, as well as brownish specimens, darker and lighter ones, fish with pointed snouts and others with blunt heads. In some the mouth was terminal; in others sub-terminal. One fact arising from the thorough-going investigation was the remarkably low gill raker count. My material even included specimens having only 18 to 19 gill rakers, and a count of 26 was surpassed only very infrequently. The fishermen were also unable to give me any answer to my question concerning the biological differences between the supposed "gangfisch" and the "blue coregonine". Supposedly they spawned at the same time and places. One of the fishermen claimed that catches in the main consist of "bastards" or ~~"highbreds~~ "hybrids" of the two "species". Previously, the only designation known was "renken". Only WAGLER was responsible for suggesting the introduction of the names current in Lake Constance.

I, myself, will for the timebeing refrain from dividing my material into "ecotypes". What I was able to examine was, to say the least, chaotic. I consider it out of the question to differentiate between ecotypes in a lake in which spawn fishing

is not known, and in which, consequently, the fishes are not caught at spawning maturity. It would be necessary to have hundreds of specimens of spawning fish of various connubii. Perhaps it would then be possible to plot variation curves having several peaks and to arrive at mean values by means of mathematical calculations. A prerequisite of this would, however, be the ability to recognize each "species" as such, in order that it may be assigned to the right curve. Under the circumstances prevailing in Lake Chiem, calculations of mean values amount to nothing more than self-delusion.

I am reproducing the following figures for illustration without comment:

According to WAGLER, the gill raker count is:
In the case of the "Lake Chiem blue coregonine": 23-34, Mean: 28.6
In the case of the "Lake Constance blue coregonine: 32-42, Mean: 36.4
In the case of the "Lake Chiem gangfisch": 20-30, Mean: 24.9
In the case of the "Lake Constance gangfisch": 33-47, Mean: 40.2.

My own measurements and counts in Lake Chiem showed the following extremes:

19 and 27

A completely sober interpretation of the findings would have to state approximately the following:
Lake Chiem - shallow lake, the mean depth of which is only 24.5 m, has tended to support the development of the "Litoralis type". Consequently, the number of gill rakers in all Lake Chiem fish is relatively small. Ecotypes with smaller gill rake filters became overwhelmed since the selection value of this characteristic in Lake Chiem was insignificant.

Lake Atter see

In contrast to Lake Chiem there are contained two easily separable ecotypes in Lake Atter see of which some material- fresh and alive- was at my disposal. The "Reinanke" (Coregonus) and the "Kroepfling"(Coregonus fera Jur) differ little with regard to shape; but they differ in color and size.

The "Reinanken"" regarding which I was well informed by Dr. Einsele and by professional fishermen of Lake Atter, mature, on the average, one year ~~sooner~~ earlier than the "Kroepflinge". Their fins are already in their youth of a darker color than those of the "Kroepflinge"; this reaches right down to the edge of the fin. Older specimens of "Kroepflinge" show a lighther edge of the ventral fin as well as slight or light yellowish tones. I had the chance in 1950 to forward to our museum a larger number of "Reinanken " and "Kroepflinge" as exhibits.

In the case of Lake Atter, see in my opinion, it concerns a parallel case to Lake Neuenburg (see and to other Swiss lakes); it contains a coregonus form which is close to Primigenius. It is not a genuine "ecotype pelagicus " judging by the gill-rakers(24-34; average 28.4); but its habits characterize it,nevertheless, as a "Schwebfelchen"(coregonus), i.e. greatly resembling the "Palée". Further, one "ecotype nanus", such as "Bondelle", derived from the large form. It has more gill rakers(30-39, average 35.9).

Seeing that the two ecotypes spawn in Lake Attersee at different times there can hardly be any talk nowadays about natural hybridization. This isolation, therefore, has definitely separated the ecotypes from one another.

Lake Traunsee.

Wagler passes over in silence - in his systematic works- the coregonus of Lake Traunsee. In the corresponding table there appear three question marks and the "Felchen" of Lake Traunsee is missing from all the survey tables. We examined and measured the following specimens from Lake Traunsee:

1. One "Grossfelchen"(coregonus(at present in the museum of natural and social studies at Aarau, preserved in 6 samples).
2. One "Zwergfelchen(dwarf-coregonus.Tr.)("Riedling" or "Rindling) ("Rindling"-coregonus fera Jur. Tr.) from the Museum of Natural History, Vienna(old alcohol samples from the collections of Steindachner).

With regard to the "Zwerfelchen" I gained the impression that it is a typical"ecotype nanus".

The "Grossfelchen"(coregonus) is of special interest because of its regular migrations, they were reported already by Haempel and others, into flowing water and that this fish even spawns in flowing water. It presents a perfect parallel with regard to the "Wanderalbock"(migratory Albock; Albock- the albula coerulea of Lake Thunersee.) and the "Bratfisch"(albula coerulea) of the upper lake Zuerichsee. The migratory coregonus of Switzerland can be classified with"ecotype primigenius". I was, therefore, anxious to learn whether this could be stated with regard to the fish of lake Traunsee. My samples are few in number and, therefore, I would like to voice my opinion with some reservation, namely, that the "Wanderfelchen"(migratory coregonus) of lake Traunsee is also a Primigenius.

In favor of this is, in particular, the number of the gill-rakers(28-36 in my samples).

Reviewing and summarizing this we can say that what I learned on trips to neighboring countries confirms my views that the coregonus of the foothills of the Alps began to divide into varieties, genotypically different. This division was of an autochthonous nature and occurred in most recent times in the geological sense; it has not yet come to an end in our days.

Summary of knowledge gained from special sections.

He who has studied our tables, will perceive, that we nowhere, in the entire area or region of the Swiss "coregonus" lakes chanced upon that"order", which would be the prerequisite for dividing the forms into species. On the contrary, the larger the material was the wider were the bounds of the variation, the more numerous were the transitions(perhaps"commutations") and the intermediary links. It is possible that few places of the system show such chaotic conditions as in the case of coregonus.

The situation was very aptly described in 1906 by O. Schmiedeknecht(The vertebrates of Europe/Jena, 1906/):

" No other"fish-family" presents such difficulties to the systematizer as the salmonidae. Due to age, sex, quality of the water, etc., such a multitude of variations, i.e. of local races, has been formed, that it is almost impossible to find one's way through this labyrinth of forms. We are dealing here with a recent"Tiergruppe"(group of animals.Tr.), which, with regard to species, has not yet fully become separated."

With regard to Coregonus O.Schmiedeknecht has this to say: " It is even impossible to trace the species of a limited area, for instance of Switzerland, where each lake harbors its own peculiar subspecies, to definite original forms. Seeing that also Great Britain, Scandinavia, Russia and northern Asia have numerous peculiar local forms, the systematization of the species Coregonus will always remain rather awkward".

On the whole we can testify that Fatio tried very assiduously and penetratively to separate and to group the forms as far as this was possible. But he paid too little attention to features caused by age. Many qualities of youthful samples, such as the relative length of the head, the size of the eyes, the circumference, the length of the fins, differ greatly from figures obtained from measurements of older specimens; in the case of the "species" of Fatio and also in the case of the "subspecies" they are very similar. Thus the picture is very confused if one does not limit oneself to fully grown and sexually mature specimens as was done recently by Dr. Dottrens. But it is at this junction- this was disclosed by our research- that there arises a special difficulty: Many specimens of Coregonus are not "grown up" at the time of the occurrence of the "first sexual maturity." They continue to grow afterwards and, therefore, their bodily proportions continue to change. In order to describe one type fully it is necessary to compare specimens of various ages. Statistic research with regard to variations and calculations regarding mean values are not fully valid as long as "annual

classes" are not dealt with separately. In this respect the works of Dottrens- especially if they will continue to consider this principle more closely-are very meritorious. It is from these "diligent" works that I expect support for my views regarding the "polytypical species"Coregonus lavaretus L.

It is very essential, this was established in the course of our research, that the "Reifungsalter"(maturing age.Tr.) of the "populations" is taken into consideration; for it gives us the key to an understanding of the many relationships between the various types. " Fruehreife"(early maturing.Tr.) "part-"populations are often inclined towards "Verzwergung" (dwarfing.Tr.), in connection with which "youthful" features are retained even in old age. On the other hand, "spaetreife" (late maturing.Tr.) kinds, in many lakes, are characterized by an intensified" Wuechsigkeit"(thriftiness.Tr.), that is to say, by a "Riesenwuchs"(giantism.Tr.). Particulars are dealt with by us in the genetic part(Section"Ecotype nanus, S 89).

We tried in our research, time and again, to clarify the ecological relations of the individual or separate forms and succeeded in that way to establish a considerable variation- range of ecology. Many uncertainties regarding the spawning periods and the spawning grounds could be dispelled; new information was obtained or gained with regard to the feeding habits and the migrations of the "Felchen" (coregonus.Tr.).

In contrast with the views of earlier authors, namely, that coregonus that have become acclimatized in strange or alien surroundings experience an adaptation on a somatic basis

within a few decades, it became plausible that the large variation-range of the "Felchen"-characteristics is based, mainly, upon a gentypical basis. This, however, is not to say that surroundings can not considerably affect the form and the color of indifidual specimens. Especially the basic color changes greatly due to the locality. Many of the color-characteristics must be studied at once after death or if possible on the living specimen seeing that the distribution of skin-chromatophores ~~are~~ is subject to great changes after death. This applies, in particular, to fish that dwell in the deep region and the coloring of which, due to the decrease in pressure as the nets are being hauled in changes beyond redognition in the shortest time.

It has become more and more evident in the course of time that the various aberrant forms- the dwarfed and the giantly, the slender and the stout, the forms with fine and coarse gill-filters- can be grouped around a type of a medium kind, which morphologically and, especially, ecologically, manifests certain primitive features and was assigned by me to the hypothetical primordial "Felchen" coregonus lavaretus primigenius. It was established with regard to this little specialized type that it, up to most recent times, even at present, is inlined to anadromous migrations, so much so that, at times, we can call it a "Wanderfelchen"(migratory coregonus.Tr.)("Palée", in certain kinds, Wanderalbock- migratory albula coerulea- Bratfisch, Weissfelchen-white "Felchen"- coregonus of lake Traunsee and others). It was after the printing of the special section that I succeeded in making a few additional observations or findings, which, because of

their fundamental importance, shall be cited here: There are several "Felchen" from the Rhein between Basel and Strassburg, which I regard as Primigenius, in the museum at Vienna. Bruckner has in 1776 in his "Merkwuerdigkeiten von Basel" (Interesting things about Basel.Tr.), without any comment, mentioned Lavaretus as a well-known fish of the Rhein in the vicinity of Basel. Between Koblenz and Laufenburg matured specimens of coregonus are being caught ~~there~~ all the time. A mature specimen was sent to me from the Augst-Wyhlen reservoir. Every year "Felchen", ready to spawn- are caught in the Rheinfall(Rhein-waterfall.Tr.)reservoir at Schaffhausen. All this-together with the cases cited on Page 96- proves to us that the "Felchen" are not the "pure lakefish" for which they were regarded earlier. On the contrary, they originally spread in flowing waters and the adaptation to lakes is a secondary development. This naturalization is not yet completed with regard to all the populations. Particulars in this respect are dealt with in the zoographic section of this monography(see Page 73). As an essential results of our work we regard the proof that forms of various lake regions, which, at first sight, are like each other differ in regard to particulars in the structure of the gill-rakers and in their ecological attitude. It is advisable not to depend too much upon the outward appearance if one intends to establish the details or particulars of the relationship. There occur, no doubt,"convergence-phenomena", which create the illusion of a closer relationship or kinship.

As an illustration I mention the "Kropfer"(coregonus exiguus. Tr.) of lake Thunersee, the "Bodenseekilch"(Coregonus acronius Rapp of Lake Constance) and the "Kilch" of Lake Ammersee, which, as forms from the deep(ecotype profundus) manifest a number of similarities. The latter, however, differ ~~greatly~~ to such an extent with regard to details that all three of ~~them~~ them must be regarded as autochthonous specializations within their" nations"(see Page 102). The same applies, so it seems, to many "Blaufelchen"(Ecotype pelagicus), which as " open water Fish" or as " Schwebfelchen"(coregonus dispersus.Tr.) disclose many common features; but with regard to details they differ from one another. Thus the most natural explanation of this fact is that in each nation the "Schweber"(coregonus dispersus. Tr.) is traced to the local Primigenius ~~of~~. The same applies also to the Litoralis.

In view of all this ~~is~~ it is always to be remembered that the "ecotypes" are always and everywhere nothing but "idealized pictures ", which we construct on the basis of our experiences, which we, on the basis of extended research, perhaps must change and reconstruct; but which, in no case, must be permitted to tyrannize us, if we do not want to do ~~vi~~ violence to Nature.

ZOOGRAPHIC, GENETIC and SYSTEMATIC PROBLEMS.

ZOOGRAPHIC PROBLEMS.

In my statements I am speaking of the immigration of the "Felchen", having in mind the "Urfelchen"(primordial coregonus.Tr.), a migratory maraena, which I have characterized as Primigenius(Steinmann, 1948) and which I regard as the original or tribal form of the present-day"Felchen". When did Coregonus arrive in central Europe? From whence have they come? What migration routes were used by them?

The just published splendid" Verbreitungsgeschichte der Suesswassertierwelt"(History of the spread of the fresh-water fauna) by A. Thielmann(1950) contains significant material to build an immigration theory aw well as the work of Walger- published in 1950-" Coregonus in the lakes of the foothill Alps, XI: Origin and Immigration of coregonus of the foothill Alps" supplies abundant material for our problems. We will deal, at least, with a few points. The interesting statements or deliberations by H. Steiner" Some faunal-geographic aspects with regard to the problem of the modificatory or genotypical differentiation of Coregonus in the waters of the northern edge of the Alps", Rev. Suisse Zool. 55(1948). What we need to solve our problem is a history of the rivers of Europe. In this respect many a detail is yet to be cleared up by geologists. The central European "coregonus" lakes belong to three river systems, namely, to the Danube, the Rhein and the Rhône rivers. When and how were these waters connected with one another at one time? When has the region of the Alpine Rhein, that of the "Hochrhein" (Upper Rhein.Tr.) lost the features or character of an upper reach of the Danube river?

When was it that these areas became tributary to the Rhein? When was the upper Rhône river, at one time the source of the Aare river, tapped and diverted into the Mediterranean Sea?

One cannot demand of us biologists that we draw a clear picture regarding the time and the route of the migrations, seeing that the geologists can provide us with so little reliable information. We will gather from the fragments what will serve our purpose:

The former course of the Danube river follwing the south-east river of the Jura mountains must be regarded as a very old river-valley, which was formed prior to the pliocene Jurassic fold. Its forerunner was the "pre-alpine 'Sammelmulde'(collecting trough or basin.Tr.) between the subsequent Jura mountains and the Alps, which were formed by the Tertiary gravel from the mountain ranges that came into existence. The primordial Danube river flowed through this depression, which ran from SW to NE, during the Pliocene period. It is possible that even during the earlier ice or glacial periods some regions of the modern central part of Switzerland continued to be tributary to the Danube river. I failed to obtain more definite information in this respect. What we know is this: During the "Riss-Eiszeit"(named after the "Riss", a tributary of the Danube. It is the time of the second last deluvial glaciation of the Alps.Tr.) the entire trough between the Alps and the Jura- that includes the entire area of Coregonus-was covered by a vast mass of ice.

This mass was so thick or heavy that temporarily glacier-tongues reached over the pass-depressions of the fold-Jura into the table-Jura valleys. The western part of the Rhein-glacier of the Riss-glacial period reached as far as the region of Waldshut, where at present the Aare river joins the Rhein river there it met with the "forehead" of the Aare-glacier. It is plain that at that time Coregonus could not exist in the central parts of Switzerland. There was no chance for Coregonus to exist under masses of ice hundreds of meters thick.

On the other hand we know that the break-through of the Rhein through the Jura, which was occasioned by the retreating erosion from the west, that gained in aggressiveness through the increasing lowering of the Upper-Rhein low plain had progressed so far already in the Riss- glacial period that the waters of the Riss-glaciers found their way westwards to the Upper Rhein depression. During the Mindel-Riss-interglacial period, at the latest- possibly earlier- the former upper reaches or bed of the Danube- draining the present-day Aare-river region- was diverted westwards to the Upper Rhein and henceforth carried its waters to the North Sea. Of decisive importance for this knowledge is the ancient- erosion-valley, repeatedly abandoned by the present-day Rhein, which can be traced from Basel via Waldshut-Schaffhausen to Radolfszell. In many places it was deeper than the present-day Rhein and is, for instance, covered with 40-50 meters of gravel at Schaffhausen and the top is covered with a moraine. The extraordinarily deep "Auskolkung"

(erosion by water.Tr.), at the latest, is to be placed in ~~to~~ the time of the great Interglacial period- the ~~xxx~~ period between the Mindel and Riss- glacial period. The Rhein river had its source at that time in the "Bodensee"(Lake Constance) region, where it struggled with the upper reaches of the Danube for the watersheds. Its gravel, according to Schmiedle(1915), can be traced as far as Stahringen. Its fountain-heads could have been located farther eastward towards the edge of the Alps.At any rate, during the middle diluvium the "Alpenrhein" (Rhein of the Alps.Tr.)- including Buenden, Vorarlberg, St. Gallen- carried its waters still in the direction of the Danube river.

These circumstances lead to some important deductions with regard to the migration of the "Felchen"(coregonus):

1. The entire area in which at the moment the "coregonus" lakes are located- we will see that the lakes of the Rhône region also belong to this area- was already prior to the Riss-glacial period connected with the Upper Rhein and was being drained towards the North Sea.
2. Also the basin of lake"Bodensee"(Lake Constance) was since the Mindel-Riss-Interglacial period, at ~~in~~ its western parts, tributary to the Rhein and not to the Danube.

This raises the greatest objections with regard to the hypothesis that the Coregonus immigrated from the Danube region. If the Coregonus came from the east then it must have happened already in the Pliocene period. That is contradicted by the fact that our country was completely covered by ice during the Riss-glacial period. The Riss-Wuerm-interglacial period can

be regarded as the earliest date of the immigration of Coregonus nus. We will deal later with the question of the watersheds during the Wuerm-glacial period. We will also show later that a much more recent immigration-period of Coregonus is much more likely.

We must insert here a word regarding the mode and manner of the immigration of the "Felchen". According to our opinion the view of a gradual settling or appropriation, in stages, of basins containing glacial waters and of reaches of rivers that lie between is erroneous. We must not forget that the "Felchen" are migratory fish by nature. F. Zschokke, almost 50 years ago, expressed himself regarding their "vagabond" nature in connection with the climatic changes of the glacial and post-glacial periods. We only have to think of the salmon which even today migrates every year from the sea to the "edge" of the Alps and then returns. The idea about the spread of the"Felchen" from the north through the ice-free belt to the mountains, which, for instance, Walger finds it very hard to accept, presents no difficulties, if one disregards the slow progress of the distribution,which depends upon causal or accidental spreading. As an anadromous migratory(vagabond?) "Felchen" the Primigenius moved in the post-glacial period- perhaps already during the Wuerm-glacial period and in the Riss-Wuerm interglacial period- through the water-ways of the melting glaciers to its spawning grounds, which one must xix visualize in flowing water or in the reservoirs near the edge of the glacier.

We must bear in mind, in this respect, the Siberian "Wanderfelchen"(migratory Felchen.Tr.) as well as the "nordische" (northern or nordic.Tr.) migratory maraena.

Let us assume that a "Schlag"(kind, sort.Tr.) of the Primigenius, possessed of wanderlust, travelled during the glacial period from the mouth of the Rhein of that time to the border of the Alps and back. I mention also the ~~MRHHHX~~ "Rheinschnäpel", which to this day migrates in the Lower Rhein and which we can regard, according to the view of Thienemann, without trouble, as a specialized race of the primordial "Felchen". Such a migratory"Felchen" could retain his migratory habits also during the glacial period. In the post-glacial period it might have proceeded further and further to the south the more the edge of the ice receded. There it could inhabit the newly formed lake basins and even, this was done by the salmon until recently, cross them in order to reach the source of the river. ~~Thexpostglaxialxxgravxlxayex~~ Afterwards there remained here and there populations in the fresh water and migrated now only from lake to lake or from the lakes to the fountain heads of rivers. The post-glacial gravel-layer more and more separated the lake-basins that originally were joined and confined them. This was the eternal, the dying migration impulse, the inner "isolationemechanism, which,as we will state later in detail, brought about the differentiation of the population. Thus, in my opinion, the question of the "immigration" of Coregonus is easily explained. For this we need no complicated suppositions regarding distant origins of the primordial"Felchen" in Finland or in the Balticum.

Is it not natural to let the "Felchen" follow the routes that are used at present by the salmon, by the eel and the river-"Neunauge"(a fish-like vertebrate, with the apertures of the snout, the eyes and the gills of which have the appearance of eyes.Tr.) - until a few centuries ago also by the sea"Neunauge, the sturgeon and the "Maifisch"(May-fish.Tr.)?

Some one will object that in this case the origin of the Bavarian and Austrian coregonus has not been explained. I know too little of the history of the Danube river and of the geology of the mountains of central Germany to participate seriously in the discussion.

Wagler, in his latest work(1950), suggests that Coregonus migrated from the Baltic Sea via the Oder river into the Danube river.

" Earlier I drew attention to the fact that at one place in the "Mittelgebirge"(central mountains.Tr.), which drain towards the Baltic Sea, there are water-courses that are separated by moderate barriers from the rivers flowing southward, to the Danube. This place is in the eastern part of the Sudeten mountains: The March and Stille Adler rivers flow southward to the Danube(Wagler has erred here: the Stille Adler river empties its waters into the Elbe basin!), the Glatzer Neisse river flows northward to the Oder river and both are separated by moderately high barriers, which are only a few kilometers in width. Perhaps it was possible to overcome this obstacle during the post-glacial period or even in the last Interglacial period."

We are asking why Wagler uses one of the highest elevations of the Sudenten mountains, i.e. the region of the "Schneeberg"(Snow mountains.Tr.), as a "gate", seeing that somewhat farther to the east the "Maehrische Pforte"(Moravian Gate.Tr.) would have made a much more natural connection between the Danube and the Oder rivers. I am asking myself further, whether this gate, which is only 310 m above sea-level, could not have earlier directed the water of the entire upper reaches of the Danube river to the Oder river so that the anadromous wanderers from the north could have reached the edge of the Alps by this route. Of course, one is inclined to think of "gates" farther to the west, i.e. of a Danube-Main connection. In that case the North Sea region would have to be regarded as the place of origin of the present-day Danube-coregonus. The final word is with the geologists. They must tell us where and when the upper Danube flowed towards the north.

A special question, which concerns the access of Danube "Felchen" to the river-area of the Rhein, must be mentioned here. It is known that the Rhein-glacier of the Wuerm glacial period carried a considerable part of its waters into the Danube basin. Thus, through the action of the glacier, connections between the Danube and the "Bodensee"(Lake Constance) -Rhein were established. The question is now whether the Coregonus, which were"at home"at that time in the Danube basin, could have migrated to the Rhein. However, it is to be emphasized that the Lake Constance region and its northern foreland or cape were completely covered by the Rhein glacier of the Wuerm glacial period.

Therefore, no "Felchen" could exist in the "Bodensee" area during the Wuerm-glacial period and the "settlement" of the "Regio bodanica" must have taken place, at the earliest, after the recession of the Wuerm-glacier. The conditions in the northern foreland of the[X] "Bodensee" as well as within the realm of the water-shed, which stretches toward the Danube are very complicated, seeing that the end-moraines of the Riss-glacial period as well as of the Wuerm-glacial period are located near the present-day water-shed. It is definite that at the greatest height of the Rhein glacier of the Wuerm-glacial period the eastern parts of the ice-masses inclined towards the Danube and, in that connection, reached as far as the southern part of lake Federsee. On the other hand, it is as certain that the western arm of the glacier belonged to the Rhein region. The "Molasse" mountain range Goerenberg(754 m) and Heiligenberg(788 m) to the north-east of the "Ueberlinger" arm is to be regarded as the general border line. The glacial masses to the south-west of this zone, which covered the region of the present-day Untersee and Ueberlingersee lakes, were drained towards the west through the old erosion gullies. Even if we would assume that the coregonus of the Danube region could have penetrated at that time directly to the edge of the glacier, which is rather unlikely for ecological reasons, they could not surmount the water-shed for at the highest height of the glacier it was buried under ice.

X Lake Constance.

Even if after the recession of the glacier they(coregonus) could have penetrated into the basin of Lake Constance at some places it must be remembered that at that time Lake Constance was non-existent, resp., that the basin was still covered with ice. When during the retreating phase first of all the western part of the area was freed from ice, this was during the so-called Constance Stage, the Rhein-Danube watershed had been pushed quite a bit to the east. This establishes the following: Lake Constance has since its post-glacial formation been draining towards the Rhein and not towards the Danube. Therefore the possibility that Danube coregonus penetrated into the Lake Constance region must be abandoned. Lake Constance, too, like all the lakes of the Rhein region, received its coregonus from the estuary region of the diluvial Rhein.

Seeing that coregonus- like any other"wanderer"- could not surmount the Rheinfall"(Rhein-Falls.Tr.) at Neuhausen, their penetration into Lake Constance must have occurred at the time, when the river was not yet flowing through the epigenetic "Umwegtal"(by-pass valley.Tr.) at Schaffhausen; but flowed through or followed its old deep course towards the west. The age of the"Rheinfall" is estimated at 22,000 years. This may lead to a somewhat plausible dating of the advance of Coregonus towards the"Bodensee"(Lake Constance.).

A rather complicated problem with regard to fauna and geography, is the occurrence of coregonus in Lake Genfersee and in Lac du Bourget.

Wagler and Thienemann are trying to solve the problem by looking for the Danube-Rhône conection via the Upper Rhein-Basel through the "Burgundische Pforte"(Burgundian Gate.Tr.) and the Saône. Thienemann(1950) believes that this migration route was still open in the late glacial or early post-glacial periods. In my opinion this explanation can not be entertained because the "Coregonus" lakes in the angle between the Jura and the Alps(Lake Genfersee and the neighboring lakes of Savoy)belonged even during the Wuerm glacial period to the basin of the Aare river and not of the Rhône river. Geologically speaking there existed until recently a water-route between Lake Genfersee and lake Neuenburgersee through which the waters of the upper reaches of the Rhône were diverted to the Aare river. In the entire course of the Aare river until the place where it joins the Rhein and in all the "young " moraines there occur the typical boulders, which the present-day upper Rhône- as a former fountain-head- carried to the Aare river. Even in the Buehl-stage of the early post-glacial period the level of lake Genfersee was more than 30 m higher than at present. The shore terraces speak an ummistakable language. Had it been a little higher than the waters of lake Genfersee would have flowed through the depression of Venoge-La Sarraz-Yverdon into lake Neuenburgersee, i.e. follow the course, which was followed by the glaciers of the Wuerm glacial period. The tapping of the Rhône- basin by an aggressive tributary of the Aare river below Geneva is of a more recent date. Lake Genfersee and the upper Rhône- with regard to fauna and geography- do not belong to the region of

the Mediterranean Sea.

The "Perte du Rhône" below Geneva forms a very definite distribution-barrier. No fish of the lower Rhône can find its way into Lake Geneva through the stream, which is partly an underground stream. For this reason alone the hypothetic migration route: Danube-Upper Rhein-Basel-Burgundian Gate-down the Saône- up the Rhône-Lake Geneva is completely impossible. The "Felchen" of the Lake Geneva region reached their habitat from the Rhein and from the Aare. This route could have still been open 20,000 years ago. Besides the aforementioned Venoge-depression the Broye-valley is also to be considered; for in geologically recent times the latter was connected with Lake Geneva via the Veveyse river(?).

By way of a summary we can say that the only migration route of the Swiss coregonus could have been the Rhein river. It is true that at one time the sources of the Danube were in Switzerland- perhaps even in the present-day French Jura. The Doubs, which remained outside the diluvial glaciation zone and because of that displays certain Danube-relics, first and foremost the "Roi du Doubs"(see also Steinmann, 1938), was at one time the pliocene upper reach or river-bed of the Danube. But all this occurred several hundreds of thousands of years prior to the immigration of coregonus and has nothing to do with our problem.

Further problems raised or mentioned by Wagler(1950) as well as the statements by Steiner(1948) assume that the "Felchen" varieties had been fully differentiated or defined prior to migrating to our region. It is impossible for me ~~to~~ to agree with the authors on this point; for my view is radically different. A discussion would be pointless, seeing that our views are entirely different.

SUMMARY.

Our immigration-history of Coregonus, in b... follows:

About 20,000 to 25,000 years ago when th... f the Wuerm-glacial period were retreating- pe... ring the Wuerm glacial period itself or durin... rm intergacial period- sdhools of the anad... tal "Felchen" migrated every year from the se... of the glacier and spawned in the"young " wa... lacier- foreland, which was just being freed ... ng that the entire course of the Aare river at th... part of the Jura range of mountains was ice-f... iness could transpire in the same way as it ha... the source-regions of Siberian rivers. From l... ersee the fish proceeded to Lake Geneva and to ... Savoy. Following the retreating glacier the wan... rants came closer and closer to the Alpine zon... he "Randseen"(marginal lakes.Tr.) were forme... ations became stationary there. Others continued ... rations or wanderings- so it seems-until historic ... increasing isolation of part-populations led to th... of the types, which will be mentioned once more i... hapter.

We just want to add that the phenomenon ... stationary in the case of "Felchen" is not an isol... recall the sea-trout, the brook-trout and the la... Chep- pia-Agone just to mention the most import... re are also forms known of the "Schnaepel", this ... of the brackish waters, which have become st... land lakes. However, great difficulties are enc... very case with regard to the systematic classif... rms.

No species have yet originated, but only nations and ecotypes, at best, that is, conjectural preliminary steps of newer species, which for the time being must be grouped in a poly- typical uniform species, namely, Coregonus lavaretus L., Trutta fario L., Alosa finta L.,....

In closing another word regarding the difficulties, which can arise with regard to zoogeography, if convergent development-processes occurred.

If the Coregonus lavaretus- as a polytypical species- is capable of producing a great variety of forms it can practice this anywhere in its present-day zone of distribution. If, however, in faunal-geographic deliberations the main argument in favor of an eastern origin of the "Felchen"race is always the fact that in the east- for instance in the Baltic region and in Russian Siberia- the greatest variety as to form exists, it can be said, as a rebuttal, that hardly anywhere there has been demonstrated a greater variety as to the form of the "Felchen" than in central Europe and, especially, in Switzerland. Nevertheless, no one will assume that Switzerland is the land of the origin of Coregonus. The variety which is manifested in one region with regard to morphology and ecology is the reflection of the variety of the waters inhabited. Ecotypes can arise everywhere- in the north as well as in the south- in an autochthone manner. If they correspond largely, so it is not to be wondered at that in the various habitats of Coregonus there occur time and again similar biotopes.

The otherwise often customary zoo-geographic method, namely, to reconstruct the history of the distribution from the systematic marks of the denizens, from their greater or lesser similarity in connection with the topography of the habitat, fails in our case, seeing that it concerns not species but ecotypes, which could spring up anywhere, if the corresponding ecological prerequisites are furnished. Furthermore, we must mention also Thienemann, who regards the Coregonus forms with a definite sub-terminal or receding mouth and protruding or extending snout, the so-called "Schnaepel" also as products of convergent development-processes. He has them originate as "Rheinschnaepel", "Elbschnaepel", "Ostseeschnaepel"(Baltic Sea schnaepel.Tr.) etc. from various "normal" races at various places. This fully corresponds with my view. The "ecotype oxyrhynchus", so it seems, occurs only in the north so far, if we are not willing to designate certain Litoralis forms with an extremely subterminal or receding mouth- for instance the "Sandfelchen"(coregonus fera Jur.) of lake Untersee- as "verschnaepelt"(schnaepelized.Tr.)

GENETIC CONSIDERATIONS WITH REGARD TO THE "ZELCHEN" PROBLEM.

Introduction.

A few common or general view points regarding the question of the origin of new hereditary features as perceived by systematizers and geneticists must be mentioned at the beginning of this section. The process, which is the object of the especially intensive research of present-day biologists, has been called by various names by various authors. They speak, in joining Darwin, of the "Entstehung der Arten", ~~exigin~~ "origin of species" or " speciation" and then they talk about "Evolution" or " Differentiation of species and races". However, they always mean or have in mind the process of the origin and consolidation of new hereditary qualities or quality-complexes. The region or realm of the origin of lower systematic units, in particular, is also designated as a "micro-evolution". We prefer the designation "intra-specific evolution", which was introduced by RENSCH. This is placed against the "Erscheinungsgruppe" (appearance-group.Tr.), which formerly was designated as a "macro-evolution. To it could also be applied the term" trans-specific" according to Rensch. The term "trans-specific" means: An evolution going beyond the species, reaching into the higher categories. This concerns, for instance, the construction of a pedigree of larger groups and similar questions.

Our special research regarding the variety in the forms of the "Felchen" of central Europe have led us, as already stated, to discard all the "new" species that were described decades ago and to recognize only the old, the species of Linnaeus: Coregonus lavaretus. Most of the varieties and subspecies, which were formerly created due to the diligence of ichtyologists, have not lost their significance, but they must be, to a large extent, re-processed and re-defined, if one is willing to yield to the demand of up to date research not simply to register the existing variety in a system but to express in it the relationships of the various separate or individual forms.

Mention will be made in the sections that follow concerning mutation and many things will be said about selection and isolation. We tried to orientate ourselves by means of the book "Systematics and the origin of species" by Ernst Mayr and also that by Rensch entitled "Neuere Probleme der Abstammungslehre" (More recent problems of the science of descent. Tr.). In doing that we gathered many valuable stimulating thoughts. Nevertheless, it must be said here and now, a geneticist or a genetically orientated systematizer, who deals primarily with mammals, birds, insects and land-molluscs, can not see the problems the way we would wish that he would see them. For fresh-water fauna has its peculiar aspects. The concept of geopraphic isolation assumes a somewhat different meaning in this research area and the

means of reproduction and of distribution are of a special kind: kind. Therefore it is not possible, without reservation, to accept all the terms of the authors, who till now dealt with these problems. In some cases, this is inevitable, the significance of the concepts or terms used will be shown by illustrations.

Coregonus lavaretus L. as a polytypical species .

Our "Art"(species.Tr.)- the European"Felchen"- is to be regarded as a "polytypical species" or as a " Formenkreis" (Form groups in a system.Tr.). We avoid the term "Rassenkreis" (race-group.Tr.), seeing that this word is being used in a different sense in animal husbandry. One could reply to our view that the various" appearance-forms" under which the "Felchen" presents himself or itself in our various bodies of water, are "modifications", i.e. changes in an original type of a somatic nature due to the environment. In this sense Mayr speaks of "ecological races" and,at the same time, rejects the term or phrase as vague.

" "No evidence exists for most so-called ecological races which would indicate whether they are merely phenotypical or whether their morphological differences have a genetic basis."

We reject the view that the shapes of the"Felchen" are somatically formed by the environment and the way of life and, in this sense, should be adapted to their biotope. Later on we shall establish this view(see Page 117) and wish to prevent at this junction that something like that would be read into our view, namely, that a polytypical

of the kind of genus Coregonus lavaretus is a community of different, in the sense of heredity, but, evidently, very closely related varieties. Under"variety" we understand in the broadest sense every change or digression from the type. In connection with this we wish that a clear differentiation would be made between"modification" and "hereditary change". We are interested in the hereditary varieties, which originated from mutation processes and were consolidated by isolation processes(see Page 115 ff). They were designated by us as "nations" and "ecotypes. The more nations and ecotypes a species forms the more its deserves the designation"polytypical."

It must now be established why the "Felchen", in particular, have attained to such a high degree of polytypism , whether special conditions in the chromosome sets(?) of individual races can be held responsible for this or whether we can point to other indications of mutative processes.

The chromosome sets of Coregonus.

SVÄRDSON (1945) and KUPKA(1948 and 1959) have written about the chromosomes of the Coregonus races. H. Ambühl, my fellow-worker, and I have examined the results that are at hand and also enlarged them and intend to publish a special work in this respect. It would lead too far and would encroach upon the work to be done if we would state the results in detail. Only a few main questions of general importance will be dealt with in passing:

The chromosome formation in the case of Coregonus, according to Svärdson, is irregular to an astonishingly high percentage. In the sets of the first fissure-cells(German" Furchungszellen".Tr.) one can, in the case of certain varieties, recognize four chromosomes in each, which correspond to each other as to shape and size. This led at first to the supposition that it could be a case of polyploid. Kupka established by using Coregonus from lake Zuerichsee that the two races, that live there, namely, the "Sandfelchen" (coregonus fera Jur.) and the "Albeli"(Albula parva.Tr.) show the ratio 2:1 with regard to the number of chromosomes (72 to 36) and that in the case of the latter the chromosomes that are like one another occur not four-fold but only two-fold. The "Edelfisch"(small "Felchen", Albula coerulea.Tr.) of lake Vierwaldstaettersee again showed groups of four, but they differed in appearance from those of the "Sandfelchen" (coregonus fera Jur.). The very characteristic SAT-chromosomes, for instance, were considerably smaller than those of the "Sandfelchen". Similar conditions were discovered by Kupka in 1950 in connection with the " Reinanken"(coregonus) of lake Attersee. Already Svärdson had found metaphase-plates in connection with nordic coregonus, which disclosed abnormal numbers of chromosomes. He estimates the number of the digressing chromosome-numbers at 20% of the cases observed. Kupka confirms this finding. We, too, agree with the two authors.

A metaphase-plate, which was analyzed especially thoroughly, disclosed a count of only 18 chromosomes. The embryo, so it seems, was developed normally and the metaphase in this question was not an isolated case; the low figure characterized the entire embryo. From this one could conclude that the haploid basic number amounts to 18 and that the forms with 36 and 72 chromosomes are diploid resp. tetraploid. Our own research points also to triploid cases. However, it must be remembered that the coregonus(in the plural. Tr.) show an extraordinary variability of their sets in the first blastomeres of their embryos. Kupka has " Allopolyploidie" in mind. He observes that if in the various coregonus races parts of the sets are identical one must expect a crossing of the morphological features. Due to him the results in chromosome research hitherto obtained support my view that coregonus lavaretus is a polytypical species and not a genus or family divided into several or even many species.

The high percentage of eggs in capable of development, perhaps also the considerable number of "cripples" in the hatching jars can perhaps partly be traced to the faulty or wrong handling of the reproduction products; but most likely the above is due to irregular mitoses. Perhaps the frequency of certain defects in adults specimens such as heterocercy, lack of guanine, the occurrence of superfluous fins or the lack of some fins can be traced to the shortage of certain chromosomes or to the failure of certain genes- eventually also to additional chromosomes as discovered by Svärdson in his preparations.

Perhaps the occurrence of hermaphrodites, so far concerning Lake Geneva and lake Bielersee, should belong to the same chapter(see illustr. 64 and Table 13).

Seeing that this game at combination can produce unfavorable and lethal combinations it can also produce genomes, which have a positive selection value. They will prove themselves and assert in the struggle for survival.

Whether alongside them also occur mutations of a different kind will, perhaps, be clarified later by experiments at hybridization.

Illustration 64. A "Felchen" hermaphrodite from lake Bielersee showing mature testicles and mature ovaries at the same time.

By and large, it seems, that the species Coregonus lavaretus L. belongs to those organisms that are passing through a splitting- up process, which almost seems to be of an explosive nature.

The question of the sterility of hybrids.

The easily accomplished cross-breeding or interbreeding of morphologically and ecologically greatly differing "Sippen"(tribes or families.Tr.) is to be regarded as a further attitude, which is peculiar to our polytypical species.

A very high degree of tolerance is disclosed in this respect. We shall mention the results of our cross-breeding experiments in a subsequent chapter. At this junction we would like to state that we in a cross-breeding experiment, which has been continued for two years, were very successful in

crossing an extreme Litoralis type with a pelagic Nanus-type. We hope, whenever possible, to continue the cross-breeding experiments until the hybrids or bastards have matured so that we, it is hoped, will be able also to examine or test the F_2-generation. With regard to a preliminary result we should to state once more that "Sandfelchen" (coregonus fera Jur.Tr.) and "Gangfish"(Albula coerulea.Tr.) can be crossed directly and reciprocally without any preceding signs of hybrid sterility.

Serum diagnostics.

The "tolerance" in the cross-breeding is matched by a great harmony or accord in the nature or character of the albumen of the various forms of "Felchen". Neresheimer and others have attempted at an earlier date to establish the relationship of the "Felchen" by the blood serum diagnosis method. Gubler, at our suggestion, repeated the experiments in Zuerich in 1948/49. We point to his publication or article in volume 1949 of the "Schweizerische Fischerei-Zeitung"(Swiss Fisheries Bulletin.Tr.) and maintain here that with pressed juices from gonads of various "Felchen"(whitefish- coregonus.Tr.) races obtained by careful selection of typical specimens during the spawning period of 1948/49. Albumen reactions were carried out using all the precautionary measures required. However, as a result no differences in the nature of the albumen of "Felchen" could be proven. The pressed juices of the various types- members of various nations were also compared- disclosed the same attitude in the "Tierexperiment"(animal experiment.Tr.).

Even if the individual kinds of a lake(ecotypes) or the "Felchen"(coregonus) of various lake regions(nations) differ greatly from one another, nevertheless, they have a common nature with regard to the albumen so much so that we are unable to detect any difference with our modern means.

SUMMARY.

In summarizing this section let us remember:
The inclination to changes of the various morphological and ecological features is very much pronounced in the genus of the "Felchen". The variety of the "Genome"(perhaps"gnome".Tr.) is also great as far as this can be established from the mitoses in the "fissuring"(splitting, perhaps.Tr.) egg. The tolerance in the case of the crossing of extreme types as well as the harmony in the nature of the albumen are amazing. This has characterized, in our opinion, Coregonus lavaretus L. as a polytypical species.

About isolation mechanisms.

In what way does the process of differentiation take place within the polytypical species Coregonus lavaretus L.?

As long as there exists complete panmixia in closed populations an accumulation of definite or certain gene-combinations will never occur. There will always be a compromise, a leveling off. Isolation-processes are necessary for the formation of new hereditary types, which develop and finally dominate a population.

Had the primordial "Felchen", which, as an anadromous wanderer, migrated from the sea to the spawning grounds of the edge of the Alps and from there back to the feeding grounds in the sea, retained this way of life there would

have been no differantiation and no formation of xxxxxx races. The formation of new hereditary types would have been prevented by panmixia, whereas changed forms could have, time and again interbred with forms that remained unchanged. It is to be assume sumed that factors within and without brought about certain changes in the behavior of the "Felchen" genus in the course of millennia. The continuity was lost; part-populations were separated from the xxx total population and abandoned to their fate, with which, each in its own way, had to deal, ~~with problem~~. The purpose of this chapter is to discuss the mechanisms of isolation. We point to a lecture, which was published by us in 1947 in the " Archiv der Julius Klaus-Stiftung", Vol. 22.

The geological-climatic bases of isolation.

At the time when the Wuerm glacial period had reached its climax the edge of the glacier stretched from the SW to the NE through the central part of Swizerland in the general direction from Lake Geneva to Lake Constance. Under the influence of the two mighty glaciers of the regions of the Aare and Rhône rivers most of the area of present-day SW-Switzerland was covered by ice. In the "Molasse"-valleys, that were formed earlier, glacier-tongues advanced every-where and piled up curved terminal moraines through which the glacial streams cut their way to the Aare river. In the places, where ice-free valley exits opened towards the main valley, there spread vast fields of fluvio-glacial stones or gravel(Niederterrassen-schotter- gravel of the lower xx terraces.Tr.), through which the Aare river and its tributaries meanderingly rolled their muddy waters. Seeing that they carried more gravel and stones

than they could handle and, therefore, built up the valley-bottoms. Their water-courses separated and "Altwasser"(dead arm of a river.Tr.) and "Stauseen"(lakes without an outlet, so it seems.Tr.). The Linth glacier piled up its gravel and stones in a similar way in the valley of the Glatt river towards the Rhein river. Under such conditions the annually ascending migratory "Felchen" found in the area of modern Switzerland, that had remained ice-free a complicated system of puddles or pools and of water-courses, of "Stauweiher"(ponds without an outlet, so it seems.Tr.) and of moraine-lakes could spawn there and return to the Lower Rhein and to sea as far as this was possible in view of the glacial conditions of the glacier-edge. When the glacier-edge retreated at the end of the Wuerm glacial period and during the post-glacial period the lakes at the edge of the Alps, that had been scooped out earlier, became exposed. Other lake basin were formed anew due to gouging out and joined, while the glacier melted, the system carrying snow-water. One must bear in mind the abundance of water of that time, the wet climate and the periodic inundations in order to understand that there still existed communications between the various river-systems. The arriving "Felchen" found a large system of waters at their disposal. There could be no thought of an isolation of individual tribes for the time being.

The conditions, however, changed as the glacier continued to melt. The system carrying snow water "dismembered" and filled up. Valley-lakes that at one time were joined to one another were separated by the "alluviums" by lateral streams.

On the other hand, the displacement of the "fluvio-glacial" towards the edge of the retreating glacier considerably increased the "erosion-power" of the run-offs. The waters" ate" into the "gravel-fields" of the foreland of the glacier, accelerated the run-off of the waters into the valleys and affected a less frequent occurrence of inundations.

It is true that migratory coregonus still penetrated from the sea to the edged of the glacier. But the route became more difficult and some of the spawning schools refrained from returning to the sea. It seems that, in particular, the brood of the "Felchen" felt comfortable in the "young" lakes at the edge or foot of the Alps and became stationary. This led to isolations. The "Teilvoelker"("part" nations) became separated into nations.

The ecological and animal-psychological bases of the isolation.

The "Sippenschwarm"(tribe-swarm. Tr.) as a mechanism of isolation.

I regard the formation of tribe-swarms as one of the most important internal isolation-mechanisms that became "active" at this time. How it occurs, how it works and what future rôle is to be allotted shall briefly be stated in this place(see also Steinmann, Rev. suisse Zool. 53, 518/1946/).

Firstly: What is a "Sippenschwarm"(tribe or tribal swarm.Tr.)?.

There are millions of fertilized eggs on a spawning ground for "Felchen", if the conditions for spawning were favorable.

One must visualize that every mature female deposits some 10,000 eggs and that the depositing of eggs or roe occurs in "company" and continues for several days, even weeks. The spawning "company" consists, based upon experience, in most cases of fish that are of the same age and of the same size. At the beginning of the spawning there often arrive younger fish; towards the end there arrive older spawners. Also the outward appearance on a certain "spawning"day often displays peculiar similarities. Thus I could observe repeatedly that practically all spawners of a certain day displayed heterocercal caudal fins, that is, some sort of "uniform-insignia" of the particular "connubium." The "Schuppenbilder"(scale-images. Tr.) also often displayed a similarity that was amazing. This supports the view that the "spawning-company" was not gathered ad hoco; but that it represents a tribal swarm.

Once the spawning has taken place the hatching will take place at a time determined by circumstances and the eggs that were deposited on a certain day will complete, in large numbers, their development on a certain day. The result is a "Brutschwarm"(brood-swarm.Tr.), which primarily consists of brothers and sisters, of descendants of one and the same connubium (perhaps:mating.Tr.)

The "Wirbeltaenze"(whirling dances.Tr.)and the dissociation according to swarms, described earlier,now take place. Part-swarms,before the yolk-sac has been consumed, break away from the overly dense brood swarm, apparently, to escape starvation and to spread over all the usable areas of the biotope.

The companies of fry that escaped from this brood swarm, remain together for the time being, feed together as tribal swarms, this, for instance, has been confirmed by "jig"-anglers, move in a gregarious manner from exhausted feeding grounds to those still intact, in the same gregarious manner they look for places that appeal to them and escape when unfavorable or threatening conditions develop(light, temperature, current, oxygen-content, etc.). Even in later life the members of ~~the~~ a tribe stay together. Von Siebold(1863) speaks very definitely in this respect:" It is a peculiarity of the "Renken" (coregonus) and of the maraena always to stay together and that specimens of the same age congregate" Our fishermen, who use nets, ~~kmw~~ know that "Felchen" are caught at a certain time and at a certain place and of a definite size. We also stated that this applies to catches during the spawning period. The tribal swarms, therefore, represent "Gesellschaften"(companies) ~~and~~ of a life-long duration, which separate occasionally and then unite again, are joined at times by "outsiders". However, in the main, they consist of brothers and sisters and, therefore, form "Inzuchtgenossenshaften"(inbreeding unions.Tr.)

The development of the tribal swarm as an isolation-mechanism favors certain gene-combinations, eliminates others, restricts in this way the free combination and the panmixia. It is possible that similar phenomena occur in the case of all the formations of swarms and schools. It is essential for the final effect that the swarms represent themselves as units. They appear not simply as a sum of items, but as organisms that have their own rules governing their existence the members of which, for the sake of the continued existence of the company do not

follow their own imperatives and often sacrifice in favor of their individual interests. One has only to observe the disciplined maneeuvring of a swarm, which has suffered a collective shock or the keeping of distance or the spread of an impulse through the entire swarm in order to understand the higher individuality of a swarm.

The functions of the company or association vary. We are interested especially in this connection in the migration as a swarm and the locating of certain spawning grounds and at a certain time. It is not established how they do it; but it is certain that they do it. It is to be assumed that certain reaction-norms are inherent in some tribal swarms by heredity seeing that they often also manifest peculiar morphological qualities. The "Schwebfelchen"(coregonus. Tr.) of lake Vierwaldstaettersee spends the winter in the "Pelagial" and fattens there, starts on his migration in the spring to the farther end of the lake and into the deep in order to spawn there beginning in Juli. Late in summer and in fall the fish return to the "front" part of the lake. A "Schwebfelchen", hitherto not observed, occurring recently in the same lake has altogether different habits. This fish spends the summer in the "Pelagial" while the "Edelfische"(small Felchen - Albula coerulea.Tr.) spawn, and in winter come to shallower places in order to spawn partly in the pelagic zone and partly at the shore. Thus every tribe has its own inherited habits, which, in the main, are retained at new"residences" as far as this is permitted by the regimen of the new homeland.

The observance of a certain spawning period, the definite migrations the goal of which, apparently, is a certain spawning ground- all this is still unknown with regard to the internal and external comditions; but the prospective significance is clear: Maintenance of tribal continuity by, if possible, elimination of alien hereditary qualities, which do not correspond with circumstances. I am of the opinion that it is essential that we no longer look upon the selection process as ah "individual-selection". The tribal swarm, as a whole, enters into competition with tribal swarms of a different hereditary constitution by means of the "Genomen"(perhaps"gnome". Tr.) represented by it. The strength or weakness of such a "Genossenschaft"(association, union.Tr.) depends upon the aptness or fitness of the individual member. The selection or choice is determined by the peculiarities of the biotope, by the ecological conditions of the locale. In this respect of concern are not only the morphological features, i.e. suitable gill-filters, size of the eyes in keeping with the prevailing brightness, that is, amount of light, but also, in a significant way, the "Instinktsicherheit" (unerring instinct. Tr.) in the choice of the place and time of spawning. A fit and populous swarm will offer the hereditary features, peculiar to it, at once by the hundreds of thousands, whereas a clan of lesser fitness may have only a few thousand "applicants"; its prospects to succeed are slimmer than in the case of the other tribe.

The "Sippenselektion"(tribal selection.Tr.), which has been sketched here, so it seems, must lead to a much faster pace of differentiation and the objections raised from time to time by geneticists, namely, that the "Felchen"(coregonus.Tr.) could not have divided in the relatively short post-glacial period in an autochthonous manner into so many different types and, therefore, one would have to admit the immigration of several "Arten"(species.Tr.), do not seem to hold water.

In order to present the differentiation process, which, in our opinion, occurred and still occurs it is advisable to cite a few instances and to illustrate or describe the behavior or attitude of "Sippenschwaerme"(tribal swarms.Tr.) which are about to split into "part-populations" that differ from one another in the ecotypical sense.

The origin of ecotype nanus.

Most of our larger lakes are inhabited, besides the "Felchen" of normal growth or size, by a dwarfed type, which even at an older age retains youthful proportions and often differs definitely from the way of life of the corresponding "Grossfelchen"(full grown coregonus.Tr.). Early maturing for spawning is characteristic of the dwarf type. By means of experimental tests, which we report elsewhere(see Table 1-8), we were able to show that the early maturing- males partly in the second year, at times even in the first year become fully mature, females, as a rule, a year- is not determined by the environment, but corresponds to a special or peculiar hereditary predisposition.

We are of the opinion that the sex hormones predominate with regard to the growth hormones. We point in this connection to the corresponding sections in our general part(12, FaszI, Pp. 164-171)in which the mature fish were examined with regard to the ratio between the weight of the body and of the weight of the gonads. If the nutrients are used to enlarge the soma instead of to produce gametes then it means two things:

1. An advantage in the struggle for existence seeing that the period of growth is considerably shorter and that the chance to survive continuously improves in view of the lesser possibility to meet with an accident.

2. As a sequel of the increased numbers of eggs the reproduction figure of the dwarf race rises. This is a considerable advantage with regard to the race of normal growth.

How is the evolution from a normal to a dwarfed type to be visualized?

Our fish-breeding plants can confirm our statement that in certain age-groups of rainbow trouts and brook trouts- this can be said also of other species of fish- individual specimens mature early. Seeing that they lived in the same way as their fellows that were of the same age and belonged to the same swarm it is to be assumed that this early maturing is not caused by the environment but is due to a peculiar hereditary basis. It is possible that it concerns a mutation. It is also possible that there are recessive characteristics disposition, which will manifest themselves time and again in a population in the case of homozygotes. Let us assume that the genotypical basis "Zwerg"(dwarf.Tr.)

had survived heterozygotically in a certain number of specimens of a normal growth or size. Year after year a certain percentage of homozygotes, this is possible, separate themselves as dwarfs, which- this is important for our argumentation- at once become completely isolated biologically, because they- and only they- spawn one year earlier than their fellows of the same age. Recessive breeding with normal specimens is, therefore, quite unlikely; for the dwarfs form their own spawning schools or swarms. Later on they, forming spawning "companies", spawn jointly at certain places. A different ecological behavior, so it seems, is often connected with the dwarfed growth; thus the time of spawning maturity, according to the calendar, is advanced or postponed. All these circumstances have the effect of isolation-mechanisms. The dwarfs unite and the best prospects exist for a speedy consolidation of the corresponding "Erbgefuege"(inheritance-structure or heredity .Tr.): An "ecotype nanus" has come into existence. The swarm of normal specimens " purges" itself of its dwarfed members, continues to mature for another year and has hardly a chance to cross or interbreed with the dwarfs.

Let us now imagine that the heredity factors which change the equilibrium between growth and maturity in favor of the latter, were predominant then even the heterozygotes will mature early and be dwarfed and only the homozygotic normal, as to growth, specimens will separate themselves from the spawning swarm and continue to grow for another year. Under these conditions the subsequent generations from the swarm of the dwarfs- homozygotic and heterozygotic- 25% of homozygotic normal specimens will be ousted; they will form separate swarms or join other swarms of normal-growth specimens.

THE EFFECT OF SELECTION.

The greater fecundity of the dwarfs will have to be regarded as a selection value. The question is whether this factor is decisive in every or all biotopes. It is possible that the large-size type prevails in the pelagic region where it is necessary to swim and to search constantly for layer-zones that abound in plankton though it may have the ~~xxxx~~ fecundity of the dwarfs. It must also be remembered that the destruction-figure of the dwarf-"Felchen", that dwell at greater depths, is greater than that of the normal"Felchen, seeing that at the bottom there lurk the predatory "Saibling"(of the Salmonidae. Tr.) and "Truesche"(a species of eel. Tr.).

Therefore, we imagine that every biotope creates its own suitable ecotype.

The ecotype nanus as a convergence phenomenon.

Seeing that processes of the kind depicted in the previous section can occur independently in any lake suitable for that we need not be amazed at the fact that the ecotypes of various regions, despite the similarity, due to the same selection-conditions, differ somewhat nation-wise. For instance, the "Gangfisch" as the ecotype nanus of Lake Constance considerably differs, with regard to shape and way of life, from the "Brienzlig" of lakes Thunersee and Brienzersee. The dwarf"Felchen" of lake Lowerzersee deviates still more. The process of dwarfing, described above, has not only affected the Primigenius-type but also

the pelagic and litoral ecotypes. Indications of this are found in the morphology as well as in the ecology of the populations. We refer to our special section, which contains numerous instances. We must emphasize onee more that, according to our view, the ecotypes develop independently in each nation, that their similarities are based upon convergence and can not be regarded as indications of a closer relationship.

In view of the importance ascribed ~~xwxdwarfing~~ in our statements to dwarfing we can not but deal once more with our most important and convincing examples. We repeat that each dwarf form, which occurs in a certain body of water originated from a "Grossfelchen"(large Felchen".Tr.), that dwells in the same lake basin. Thus, for instance, the Coregonus exiguus, created by Fatio as well as the "Gangfisch" (coregonus lavaretus L.Tr.), according to Wagler,embraces heterogenous types, which are not related directly to each other, but only indirectly.

We compare now:

Bodensee(Lake Constance)	Gangfisch	Blaufelchen (Albula coerulea)
Lake Vierwaldstaettersee	White fish	Edelfisch (wartmanni nobilis)
Lake Neuenburgersse	Bondelle	Palée
Lake Geneva	Gravenche	Féra
Lake Walensee	Albeli (Albula parva)	Blaalig (coregonus wartmanni dolosus).
Lake Lowerzersee	Felchli (coregonus lavaretus L.)	Balchen (coregonus schinzii(?)
Lake Attersee	Kroepfling (coregonus fera Jur.)	Reinanke (coregonus)

We could add to the above instances; but in some cases we lack sufficient data that could be introduced as evidence. The "Albeli" of lake Zugersee and the "Haeglinge"(Coregonus lavaretus L.nat.l indimacensis, oekot. nanus) of lake Zuerichsee are practically extinct today. Thus we shall restrict ourselves for our thesis to the 14 varieties mentioned by us.

Gangfisch(coregonus lavaretus L.) and Blaufelchen (Albula coerulea).

Much has been said about the so-called "genus-independence" of the "Gangfisch" of Lake Constance. Let us put the Wagler differentiation diagnoses against each other:

	Blaufelchen	Gangfisch
Gill rakers	30-40	35" to more than 40"
Color(basic color)	more or less dark blue, green, less frequently lighter, more or less blackened (especially pectoral fin)	less frequently blue-green, mostly more or less pale-olive
Fins		blackened a little
Eye	small, mean value 3.5% of body length	large, mean value 4% of body length
Shape of snout	No data	Alternating, in most cases a sub-terminal mouth

	Blaufelchen	Gangfisch
Abwachs(growth increase) (according to Dahl Lea)	1,2,3,4,5, year 10 20 28 34 38 cm	1,2,3,4,5 year 9 17 22.5 30 cm
Location	Open water	Open water (shore and close to bottom)
Spawning time	..short, 10-14 days	long, often lasting months
Spawning place	..usually in the open	- shallow water or close to bottom in deep water.

It is rewarding to study the details of the Table somewhat closer. The density of the gill-rakers- expressed by the number on the first arch-will not make it possible to establish a radical difference. Neither will the basic color, which varies or changes from individual to individual and, according to the results obtained from our breeding experiments, is subject to great fluctuations during the life-time of an individual, be of much help. The coloring of the fins is a very unreliable characteristic. We had old "Gangfische" with very dark fins and young "Blaufelchen" with very light-colored fins at our disposal. Seeing that the sexually mature "Gangfische" are younger than the sexually mature "Blaufelchen"(early maturing!) their fins, on the average, are lighter of a lighter color. The same applies to the size of the eyes, which depends, to a very large extent, on the age of the individual. Neither can one, according to Walger, rely upon the shape of the snout. What remains with regard to the division into genera is pretty flimsy, namely:Growth or increase and spawning habits. The unbiased person will come to the conclusion that the "Gangfisch" of Lake Constance is the early maturing, dwarfed form of the "Blaufelchen"(Coregonus wartmanni Cuv.)

Albeli (Albula parva) and Edelfisch (coregonus wartmanni nobilis).

The same applies to the "Edelfisch" and the "Weissfischli" (Albeli) of lake Vierwaldstaettersee. Quite frequently, during our research, we held in our hands specimens, which could have been designated as small-size "Edelfische" or as large-size "Weissfischli". The dwarf-race has a few more gill-rakers- in the center- in comparison with the large-size form.

It is interesting to note that the "Edelfische" mainly spawn in summer, whereas the "Weissfischli", besides the summer-spawners, has also winter-spawners. The genuine"Edelfisch" is seldom as blue as the "Blaufelchen" of Lake Constance, with which it is identified by Walger. With regard to the common basic color and the orange coloring of the pectoral fin it is similar rather to the "Weissfischli", especially to the older specimens of this dwarf-tribe. The "Grossfelchen"(large "Felchen".Tr.) and the "Kleinfelchen"(small"Felchen".Tr.) of lake Vierwaldstaettersee are characterized, in later years, by an especially dark pigmentation of the fins. There are significant differences in the way of life of the two varieties, with the exception that the "Weissfischli", i.e. some schools, permanantly or constantly dwells at greater depths in the lake. The "Abwachs"(increase, growth.Tr.) is altogether different seeing that the "Weissfischli" attains maturity, in most cases, already during the second year, whereas the "Edelfisch" becomes a spawner, to say the least, 1-2 years later. There is therefore no reason to object to the assumption that the "Weissfischli" is a dwarfed "Edelfisch".

Palée and Bondelle.

For a long time the Palée and Bondelle of lake Neuenburgersee were regarded as one and the same fish; many, even today, believe that the Palée is an old or adult Bondelle. M. Vouga, the exceptionally experienced inspector-general, at Neuenburg, has repeatedly told me that he can not tell,

as far as outward appearance is concerned, a young Palée from a Bondelle. As an alternative he simply opens the fishes and examines the development-stage of the gonads. If the ovaries or the testicles of a fish, having a length of 25-30 cm, are undeveloped then we are dealing with a Palée, if not the fish is a Bondelle. Professor O. Fuhrmann has repeatedly admitted to me that he knows of no definite morphological differentiation-characteristics between the Palée and the Bondelle. However, our Tables show that the Bondelles have a few more gill-rakers, in the center, than the Palées. A definite line, such as Fatio was to have found, certainly does not exist. Dottrens and Quartier have shown by means of extensive statistical material regarding variations that the mean values for the two "Sippen" (tribes. Tr.) often differ. However, this latest research discloses that the two types again and again "overlap". They are definitely different genotypically; but there is no discontinuity, which would contradict the assumption that the Bondelles are dwarfed Palées.

Fera and Gravenche.

The same attitude might apply to the Féra and Gravenche of Lake Geneva. Unfortunately, the "old" Gravenche, as described by Jurin and Lunel, seldom occurs today. But by means of museum pieces or exhibits, which we were permitted to study, especially the original material by Fatio, which is kept in the Museum d'Histoire naturelle at Geneva- we came to the conclusion that, with the exception of the somewhat larger pectoral fins, their poorer "Abwachs" (increase, growth) can be regarded as the only differentiation-characteristic.

There is great agreement in the number of scales; with regard to to the number of gill-rakers it can be said that the average of the Gravenche is slightly above that of the "Féra". It is, therefore, may to assume that there exists a close kinship between the Féra and the Gravenche. The view that the Gravenche is identical with the "Kilch" (Salmo maraena media Hartm.Tr.) is completely wrong. This is assumed by certain research workers by reason of several external features.

Albeli and Blaalig.

The Albeli and the Blaalig of lake Walensee are regarded as closely related because of the corresponding number of scales and of gill-rakers. The "Albeli" attains, in most cases, maturity during the second winter of its life-span and has very large gonads. The large eye of this fish is especially striking. But the "Grossfelchen" of lake Walensee has also exceptionally large eyes. This is a further indication that the "Zwergfelchen" descended from the "Grossfelchen" of the same lake.

The "Zwergfelchli"(dwarf"Felchen".Tr.) of lake Lowerzersee.

The "Zwergfelchli" of lake Lowerzersee is one of the most remarkable cases. It was discovered only a few years ago. The lake is connected with lake Vierwaldstaettersee by means of river of a few kilometers in length. It can be assumed that migratory "Felchen"- in this case they would be "Balchen"(Primigenius-type.Tr.)- penetrated from there into lake Lowerzersee. There is no information available regarding the stocking of the lake with fish. No information has been received regarding the occurrence of "Grossfelchen" in this body of water.

The "Felchli" of lake Lowerzersee is to be regarded as an early maturing dwarfed form of the "Balchen", which differs from all the Swiss dwarf-"Felchen" by its extraordinarily dark color, the small number of gill-rakers and the clearly or definitely sub-terminal mouth. On the other hand this "Felchli" bears all the features of dwarfed growth: A large head, large eyes, long pectoral fins. It is clear that this dwarf can not be closely related to the "Weissfischli" of lake Vierwaldstaettersee; this fish developed as an autochthonous race in lake Lowerzersee.

I will not deal here with the foreign parallel cases-especially with lakes Attersee and Chiemsee. Nevertheless, I refer to the corresponding section in the special part(see Pp. 60-66).

This illustrations will suffice.

It seems that mutative changes, which lead to dwarfing, occur also in the case of other genera of fish. They seem to prove themselves in many waters in the struggle for survival. Large schools or swarms of dwarf-"Felchen" are often mentioned in literature. At times they border on the fabulous. Quite recently a fisherman from the interior of Switzerland reported to us that he, once again, had caught more than a centner of dwarf "Felchen" in one haul. The dwarfed growth or size manifests itself more in close swarms than in loose ones; this is due to peculiar circumstances. We must also bear in mind that the "Abwachs"(growth, increase. Tr.) depends not only upon the genotypical factors but also upon the environment. We mention here the competition for feed and perhaps also the increased mobility caused by the mutual stimulus of adjacent "swimmers."

Fluctuations regarding the numerical strength are reported from lake Thunersee. Alternately the "Kleinfelchen" and then the "Grossfelchen" dominate. If the latter dominate then the "Abwachs"(growth, increase.Tr.) of the "Kleinfelchen", whose numbers have grown smaller, is more favorable. The average size of the individuals grows smaller when the numbers of the swarm grow larger. Something similar applies also to the "Felchen" of other lakes. This can be learned from the special section.

After having stated our views regarding the ecotype nanus, which we formed on the basis of our studies of the non-geographic, intra-specific evolution, we will now deal with the circumstances in which, presumably, the remaining ecotypes were consolidated.

First the least "specialized" ecotype primigenius. The "Wanderfelchen"(migratory Felchen.Tr.) is, no doubt, the most original or primitive among the ecotypes. Its individual "Sippen"(tribes.Tr.) differ little from one another - morphologically or ecologically. It can be stated briefly what we have to say regarding the individual nations of the ecotype primigenius. They occur not only in a lake but also in flowing water- at least, in the vicinity of the estuaries of brooks- and feed- depending on conditions and seasons- upon shore and bottom organisms, then again upon plankton; they are ubiquitous, vagrant, over and above, frequently they join other types and share their "life". Regardless of all the variation in form and way of life there are no extremes in any direction.

The Primigenius proves itself always as an intermediary form. It is very likely that also the "Flussfelchen"(river-Felchen. Tr.) belong here, which as reported by Baldner in 1666 - " spawned in the Christmas month in the rigorous water upon rock-bottom" at Strassburg. They, according to Leuthner(1879), occurred in considerable numbers around 1860-1880 in the Rhein between Basel and Strassburg. Perhaps, they can be regarded as the last "certified" descendants of the true original "Felchen"(see also Page 69).

Let us deal quickly with the individual nations:

1. Natio rhodanensis:"Féra": A typical intermediary form, occurs temporarily in the west("petit lac"), later in the year it migrates eastward up to the Rhône estuary, that is, carries out extensive horizontal migrations. They spawn primarily in the deep waters, but partly also in the litoral of the plant-belt.

2. Natio jurassica: Palée: Somewhat smaller and slimmer than the Féra, otherwise similar, divides into two morphological groups, which can not be separated, namely:" Palée de bord" and "Palée de fond", with various spawning grounds and spawning seasons, is definitely possessed of wanderlust(Fatio:" Instinct migrateur plus développé"). The fish proceeds from lake Neuenburgersee through lake Bielersee down the Aare river and occurs off and on at Aarau, in small numbers even at Brugg.

3. Natio intermedia: "Ballen"(coregonus lavaretus.Tr.) and the so-called Albeli in lakes Greifensee and Pfaeffikersee: Disregarding the " Ballen" of Sempach of "the old style", which, as far as we can ascertain today, somewhat approached the ecotype pelagicus, the "Felchen" of the central lakes are designated morphologically as intermediate forms. They spawn in

shallow water. The mouth is slightly sub-terminal in most cases; the gill-filter is medium-fine. It is possible that these types are not as strongly or greatly inclined to wander as the primigenius nations of larger bodies of water. The brooks, which flow into and out of small lakes, mostly carry little water and are not suited to entice fish to wander. Some fishermen, however, report that the preferred spawning grounds are located at the estuary of brooks.

4. Natio arurensis: The "Albock of lakes Brienzersee and Thunersee. It is a typical Primigenius, rather slender, the mouth is terminal or slightly sub-terminal, the head is not overly pointed, of a great wanderlust, commutes between lakes Brienzersee and Thunersee and ascends the Aare river as far as the vicinity of Bern; the fishermen at Interlaken speak of it as "Wanderfelchen"(migratory "Felchen".Tr.).

5. Natio riusensis: It is the Albock of Zug and the so-called "Balchen"of lake Vierwaldstaettersee. They are vagrant types of medium size, clearly differing from the true "Sandfelchen" by the considerably closer gill-filter and the head, which is more pointed.

6. Natio lindimacensis: The "Bratfisch" (Albula coerulea.Tr.) of lakes Zuerichsee and Walensee. Morphologically it occurs as an intermediary form, of a great wanderlust, passes in large numbers through the opening in the lake dam at Rapperswil and ascends especially during the spawning period the channel between the lakes Zuerichsee and Walensee and into the Linth canal and, while spawning, has occurred in flowing water.

7. Natio bodanensis: The "Weissfelchen". It is a "Felchen" of medium size, dwelling in lakes Untersee and Bodensee(Lake Constance.Tr.), vagrant, spawns also in flowing water, descends as far as the Rhein at Schaffhausen, perhaps as far as Basel (see Steinmann, 1948.).

Our ecotype Primigenius, along the entire line, has been proven to be a "primitive." Its nations, due to their thriftiness and their behavior during the spawning period, differ from one another. We shall once more mention the distinguishing features of the gill-filter. The latter is neither broad nor narrow, neither delicate nor robust, neither very long nor very short. The "Feinbau"(structure, texture.Tr.) of the "Dornenskelett" (raker-skeleton.Tr.) is regular. The position of the mouth is subject to certain fluctuations. Besides the forms with a terminal mouth there occur also specimens, which disclose a tendency towards a sub-terminal mouth. There are no real slender specimens, neither are there any stocky ones, compressed laterally.

It is easy to assume that the "Urfelchen"(primitive "Felchen".Tr.) did not undergo a far-reaching specialization when it migrated to smaller lakes, i.e. to lakes, where there had been no special development of various biotopes. The fact is that the "Felchen" of the central lakes are fairly uniform. We now present the data regarding the size and depth of the lakes that are of concern:

	Maximal depth	Area
Lake Sempachersee	46 m	14.4 sq. km.
Lake Baldeggersee	34 m	5.2sq. km.
Lake Hallwilersee	27 m	10.3 sq.km.
Lake Pfaeffikersee	18 m	3.2 sq.km.
Lake Greifensee	17 m	8.6 sq.km.

All these lakes have rather wide or broad beaches and, therefore, an open water zone of any extent was never formed. They are suitable habitations for Primigenius.

Ecotype litoralis.

Part-populations, which primarily inhabit the "shallower" shore and the slope feed mainly upon organisms of the litoral, to which they are predestined by their primitive nature. The "Wanderfelchen" of flowing water feeds also upon members of the fauna of river-beds and river-banks, i.e. primarily upon molluscs, crawfish or lobsters and insects. However, somewhat different conditions predominate in the litoral of the lakes. The ice-bound condition in winter entails periods of "fasting" or imposes dislocations. The abundant feeding during the warm summer time, especially effective in the litoral, furthers growth and accumulation of fat. Therefore, there are great differences in the intensity of winter and summer feeding and the utilization of feed. This is also recognized by the big differences in the summer and winter growth-zones of the scales. Among the various heredity-structures, which were contained in the primitive immigrating Primigenius, there were some that were better suited to meet these special or peculiar conditions than others. Great voracity, for instance, and corresponding rapid growth were of selection value. Sensitivity

to temperature and early maturing had a negative effect. During the selection process the suitable element survived, what was unsuitable was eliminated. Even at present Primigenius here and there joins as an immigrant and obliterates the peculiar distinguishing features. For instance, there are many intermediary forms between "Sandfelchen"(coregonus fera Jur. Tr.) and "Weissfelchen"(coregonus bodanensis.Tr.). We know of tribes of "Sandfelchen", which during the spawning period- much the same as Primigenius-proceed to running water; whereas others prefer the biotope of the surf-zone, which is similar to that of running water. A more robust gill-filter apparatus is in keeping with the consequent restriction to feed on the bottom, i.e. suitable features have a chance to survive, whereas individuals equipped with longer and slimmer rakers are sacrificed to selection. One can imagine that the slimmer rakers that occur in population, when swallowing hard morsels of food can not meet the demand made upon them. The members of the Litoralis group often enough show worn, deformed and mutilated rakers. A study of the texture of these organs discloses a considerable variety. In this case we do not believe in somatic changes but in "small mutations" and refer to the number, direction and size of the cartilageous transverse ridges, to the varying length and size of the longitudinal ridges, to the arrangement of those cartilageous rings, which serve as a "setting" for the small teeth and also to the number and size of these small teeth.

However, all this changes from individual to individual and from tribe to tribe and in this way forms the material where or with which the selection process can start to breed that which is adapted to the feed supply of the moment.

If in some Litoralis-populations the caudal peduncle is growing shorter one must bear in mind that the effort at swimming of primitive"Felchen", which feed unhurriedly upon submerged plants, in potamogeton-forests and Chara meadows, is radically different from that of the pelagic plankton-hunters which swim about in swarms without stopping. What may be of selection value in one biotope is immaterial in another.

The correlation between the growth of the upper jaw and the lower jaw is an especially significant phenomenon. These correlations seem to be determined genotypically, regardless of the fact that the size-ratio of both jaws is developed not until the growth of the breeding"Felchen" during the first months of their life cycle. We recall that not infrequently one meets with malformations, which must have been brought about by interference in the correlation of the growth of the jaws. This points to the lability or inconstance of this distinguishing feature. In some Coregonus tribes we came across specimens with an oral opening slightly"oberstaendig" (perhaps the oral opening is located on the upper side of the snout and somewhat back of the point or tip). This feature

has developed into a specific distinguishing feature of the "small maraena" of the north, whereas in the case of our small "Felchen" it occurs only sporadically. We have no doubt that the correlation of the length of the jaws is determined in the "original material", namely, that it concerns genotypical differences, which, as long as there is panmixia, compete freely. If a part of the population adopts life in the litoral then heredity-features will manifest themselves which are suited for bottom-feeding, to suck in mud, to pick off organisms from rocks and from reeds. Thus the sub-terminal mouth will consolidate in the Litoralis-races; for it characteristic of them, whereas it occurs only sporadically in the Primigenius -populations.

Ecotype pelagicus.

The populations of the genuine "Schwebfelchen"(coregonus. Tr.) are confined or restricted to the larger lakes. The type, that is best known and best studied is the "Blaufelchen" of Lake Constance, formerly known as Coregonus wartmanni. We call it today by the name of Coregonus lavaretus L., oekot. pelagicus, natio bodanensis. In comparison with the Primigenius of its region, i.e the "Weissfelchen," it displays the following distinguishing features: A slimmer shape, a head more pointed, a closer gill-filter, darker fins when old. We must visualize that in those populations, which existed in the open water and at a distance from the shores and whose basic food was the animal plankton of the pelagic region, there accumulated heredity-features and maintained themselves that were adapted to to ceaseless swimming, to hunting for plankton-crawfish...

Other tendencies, where they, perhaps, could assert themselves, were eliminated in the struggle for survival and gene-groupings were consolidated or eventual mutations gained the upper hand, which were adapted to the particular environment. In the case of the "Blaufelchen" of Lake Constance the "Schweb"populations(perhaps something like the basking-trout, i.e. staying close to the surface of the water.Tr.) in particular avoided the litoral zone to such an extent that they spawned at a distance from the shore and let the eggs sink to the bottom. It is characteristic that in other lake-basins the process was not carried that far. Primigenius, which possesses extraordinary powers of adaptation took over in some part-populations that are not separable morphologically, the rôle of the "Schwebfelchen"(coregonus lavaretus L.Tr.). Thus we are unable to distinguish, for instance, in lake Geneva or in the Jura-foothill-lakes a special ecotype pelagicus judging by the shape. Even the"Schwebalbock" of Natio arurensis can not be definitely separated from Primigenius. In that region the members of ecotype nanus take over the rôle of the "Schwebfelchen", whereas swarms of medium size(?) predominate in the open-water region. Perhaps something similar applies to the smaller variety of the Sempach "Ballen" (coregonus lavaretus.Tr.), which belongs to the Nation intermedia. On the other hand, we meet larger, genuine "Schwebfelchen" in the eastern regions. The Reuss-region displays the "Edelfisch"(coregonus wartmanni nobilis.Tr.) as a typical Pelagicus, which is close to Primigenius in the morphological sense. However, it has a very narrow gill-filter, differs from

the "Blaufelchen" of Lake Constance by its color-features and spawning habits: The "Edelfisch" is a summer-spawner and already in early summer descends into the great depths of the lakes, whereas in winter it stays in the pelagium.

The "Schwebfelchen" of Natio lindimacensis displays a different behavior. The "Felchen" of the ecotype pelagicus that were caught in lakes Zuerichsee and Walensee are best named as "Schwebblalig". This name is used by the fishermen. Already Fatio described this type as extermely variable and attached to it the "subspecies" name dolosus. The Geneva scientist believed that cases of hybridization occurred in connection with other tribes, the limits of which can be fixed only with difficulty. His attempt to classify the coregonus of Zuerich, in our opinion, failed. His findings as well as our own research indicate that besides the migratory type(Primigenius), which we identify with the "Bratfisch", there exists a more stationary form of a wide variety-range the extremes of which, on the one hand, towards the ecotype litoralis and, on the other, towards the Pelagicus. The types, however, never attained to a real consolidation. It is interesting to note that in lake Walensee the "Schweber" (perhaps "baskers".Tr.) and the "Grunder"(Sandfelchen-coregonus fera Jur.Tr.) differ more clearly from on another than in lake Zuerichsee. The "Schwebfelchen" of lake Walensee discloses clear differentiations in the direction of Pelagicus and thus is similar, at least in shape, to the "Blaufelchen" of Lake Constance, which was mentioned above.

It is strange to say that up to date we have hardly any information regarding the spawning habits of the fish just mentioned.

Ecotype profundus.

The habitation of the Litoralis-tribes is, in general, restricted to the "Halde"(slope.Tr.). However, the "Sandfelchen" occurs at times also at somewhat greater depths in Lake Constance and in lakes Vierwaldstaettersee and Thunersee. In the catches of Lake Constance fishermen I have repeatedly observed young "Sandfelchen", which lived together with " Kilchen"(Salmo maraena media Hartm.Tr.). We regard the "Kilch" of Lake Constance as a descendant of the "Sandfelchen". Time and again there occurred in lake Untersee specimens which hardly could be regarded as true " Kilche"; but must be viewed as transitory links between Litoralis and Profundus- eventually also between Primigenius and Profundas. In general, "Kilch" represents a well-consolidated type, especially in Lake Constance. Something similar can also be said with regard to the "Kropfer"(coregonus exiguus. Tr.) of lake Thunersee. The latter discloses beside certain startling similarities also significant differences, especially in the structure of the gill-filter. Thus it can not be assumed that there exists a direct relationship between the two Profundus-types. The "Krppfer" of lake Thunersee derived from the "Albock" of lake Thunersee. Therefore it is an autochthonous formation within Natio arurensis.

The "Tiefenfelchen"(Felchen of the deep.Tr.) of lake Vierwaldstaettersee- the "Sommerweissfischli"(summer-white-fish".Tr.) still more clearly disclose their origin within Natio riusensis. Their extremely fine gill-filter identifies them as descendants of the "Edelfisch"(coregonus wartmanni nobilis.Tr.), which- regardless of the indications of dwarfing- they resemble quite a bit. They dwell, almost exclusively, in deeper waters and feeds always upon bottom-feed; this was established when stomachs were examined. It is, however, possible that at certain times of the year they move into water of lesse depth and temporarily feed upon plankton. This can also be said about the other dwarf-Felchen, the "Winteralbeli". Exactly the same applies to lake Walensee where a "Bodenalbeli"(a summer spawner) is faced by a "Schwebalbeli" (a fall and winter spawner). In this respect we have established that all these "Felchen", who dwell in the deeper region, including "Kilch" and "Kropfer", are, to a certain extent, inclined to dwarfed growth. Nevetheless, they are very well fed, partly even extremely well,. This can be traced to the fact that they accumulate much fat, even the time of maturing. When they ascend from the deep they are, naturally, very frail. The color of the body and the sooty color of the fins soon fade away. The fish look pale, especially if the surface temperature of the water and that of the atmosphere are considerably higher than that of the deep. Their frailty was caused by the difference in pressure. In most cases they are very "trommelsuechtig"(suffering from bloatedness.Tr.).

The large eyes are to be regarded as a special distinguishing feature of the Profundus-type. The clearly sub-terminal mouth is also a typical feature.

We must visualize that in part-populations that remain for a long time or permanently in the deep of the lakes these two distinguishing features are consolidated by selection. Why coarse gill filters were developed in Lake Constance and in lake Thunersee, whereas in the lakes Vierwaldstaettersee and Walensee they are fine. This is still unexplained. We believe that it is the effect of the origin of Profundus from various ecotypes. It is assumed that most likely a Pelagicus-Profundus can be told from a Litoralis-Profundus. It is a matter of regret that it is so difficult to obtain definite information regarding these deep-lake fish that are caught infrequently. It is possible that these two Profundus-groups are also characterized by different feeding habits. It must be emphasized once more that it is not to be assumed that all the narrow-filter types are strict plankton-eaters and that all coarse-filter types consume nothing but bottom-feed. Willer and Thienemann have adduced exceptions in the case of Coregonus from the Baltic Sea. Time and again there occur entire populations, which, contrary to the rule-can absorb coarse food with fine filters and fine or minute food with coarse filters.

OUR ATTITUDE TO SYSTEMATIZING THE " FELCHEN".

It is clear that there exists a practical need to give precise scientific names to the "Felchen" kinds that for decades and centuries have been designated by the fishermen by"trivial" (popular.Tr.) names.

I very well understand the somewhat impatient attitude of Walger in the "Felchen" section of the "Handbuch der Binnenfischerei"(Handbook of Inland Fishing), where he accuses me of tearing down what others had built up with much effort, yet,notwithstanding, I were unable to present or create a usable system. In defending myself I must, first of all, express myself regarding the system in general and the Salmonidae-system in particular.

As long as the system had to cope with the task of providing separate names for the appearance-forms of nature that can be distinguished, i.e. as it were to"sort out" the products of nature the "survey "catalogue, which had to suffice the expert and the lay-man, was the most desirable ideal.

But as soon as the genera came to be regarded as changeable or inconstant, when they were regarded as the products of a development-process one had to accept the fact that no significance was attached anymore to the taxonomic units within the various animal and plant groups. There is no doubt that many animal and plant families are composed at present of well definable, easily distinguishable species. However, it can not be denied that in other families chaotic conditions prevailed which could not be mastered even by the most intensive research.

Here there is strict order, no possibilities for cross-breeding and interbreeding, well consolidated gene-combinations, a monotypical character of the populations, discontinued variety. There are transitory forms, changing gene-combinations, a possibility for the "bastards" to mix successfully among themselves and with the parent-forms, a polytypical character of the populations, a continuous variety. In order to emphasize this once more we have presented the variability of the gill-rakers on Page 105.

It is impossible in the second case to apply the customary species-conception to the separate or special types. We must refrain from establishing genera, which have not yet been separated in a satisfactory manner from one another. Even if the populations under present-day conditions are no longer being intermixed we must, in order to be consequnet, continue to talk of "Lokalrassen"(local races.T_r.) until physiological reasons are produced that experimental cross-breeding is impossible.

We now must raise the question whether the central European "Felchen" the variety or multiplicity of which has "engaged research and kept it in suspense" for centuries, are to continue to form a "Genus" with such and such a number of "species" in the old sense of the Linnaeus systematics or whether we must recognize the new concept of the "polytypical genus" that can only be subdivided into "local races" (nations) and"biological forms"(ecotypes).

In order to make our own posttion still clearer we must, once more, deal with the opinion of the research workers, who dealt with the "Felchen". In this respect we can restrict

ourselves, in the main, to Erich Wagler, who collected the somewhat uncertain views of his precursors (see 12, Fasz. 1, Page 123.).

(Table on Page 105).

Range of variety and average number of gill-rakers.

Lake.	Vulgar(common) name.
Thunersee	Kropfer(coregonus exiguus)
Bodensee(Lake Constance)	Kilchen(coregonus acronius Rapp)
Lake Constance	Sandfelchen(coregonus fera Jur.)
Vierwaldstaeetersse	Balchen(primigenius)
Neuenburgersee	Palée
Aegerisee	Balchen
Greifensee	Albeli(albula parva)
Walensee	Grunder(coregonus lavaretus L.)
Lake Geneva	Féra
Thunersee	Balchen
Zugersee	Ballen(coregonus lavaretus).
Lake Geneva	Gravenche(Salmo maraenula (Bloch)
Pfaeffikersee	Albeli
Import	Grosse Maraena(large maraena)
Lac du Bourget	Bezoule
Neuenburgersee	Bondelle
Sempachersee	Ballen
Walensee	Schweber(coregonus dispersus?)
Bielersee	Pfaerrig
Hallwillersee	Ballen
Brienzersee	Kropfer
Zuerichsee	Albeli
Lake Constance	Weissfelchen(Coregonus bodanensis primigenius)
Thunersee	Albock(coregonus lavaretus)
Lungernsee	Felchen(coregonus)

~~Xhamsee~~ Walensee	Albeli(Albula parva)
Vierwaldstaettersee	Edelfisch(coregonus wartmanni nobilis)
Alpnachersee	Schwebfelchen(basking Felchen?) (coregonus dispersus)
Lake Constance	Blaufelchen(coregonus dispersus)
Sarnersee	Felchli(coregonus)
Lac du Bourget	Férit
Zuerichsee	Haegling(coregonus lavaretus L.)
Thunersee	Brienzlig(coregonus)
~~Virewaldstaettersee~~ Vierwaldstaettersee	Weissfisch(whitefish)
Brienzersee	Brienzlig
Lake Constance	Gangfisch(Albula coerulea or coregonus lavaretus L.)

Range of variation and averages of gill-rakers.
According to Fatio enlarged and revised.

ATTItude towards "polyphyletic" systematics.

Wagler builds his various systematic works, to which we have referred repeatedly, upon the assumption that the entire morphological and biological multiplicity of the "Felchen" of the "foot-hill" Alps could be traced to a uniform scheme, which he regards as the expression of a true specific diversity of four autochthonous genera of "Felchen" (see 12m Fasz. 1, Page 125).

This "tetraphyletic "theory is, so it seems to me, growing more and more untenable. I can not but point out a few of the weakest points of the argumentation of Wagler.

First of all we must remember that the tetraphyletic systematics, which crops up time and again since the time of Mangolt and Gessner, is not even tenable for Lake Constance.

"Blaufelchen"(coregonus wartmanni Cuv.), "Gangfisch(coregonus lavaretus L. nat. bodanensis, oekot. nanus); "Sandfelchen" (coregonus fera Jur.) and "Kilch"(salmo maraena media Hartm.) are to be recognized as the main types and could represent the most important tribes of the "Felchen" of Lake Constance. But it became evident that besides them exists, at least, one if not several other tribes, which can not be placed in the system. The details or particulars were stated in the corresponding passages of the special section(Lake Constance). The simplifications by Wagler correspond still less if we want to compare the types of Lake Constance with those of other bodies of water.

We will start with the large "Schwebfelchen"(coregonus dispersus) of French Switzerland. It is amazing that Wagler gives hardly any attention to the lakes of southern Switzerland and those of neighboring Savoy, which contain large stocks of "Felchen". His eyes are always fixed upon Lake Constance and he tries to apply all the other bodies of water, regardless of the costs, the views he gained there. At this juncture we must state that already at the time of Cuvier there existed very useful descriptions of the Féra of Lake Geneva, of the Gravenche, the lavaretus, the Bezoule as well as of the Palée of lake Neuenburgersee. I recall the excellent monographic works of Jurine and the splendid work of Lunel.

No one will doubt that the "Felchen" of the "French" lakes, because of their shape and way of life, are to be regarded as "Schwebfelchen"(coregonus dispersus), if he knows the circumstances.

It is true that these tribes of the "Blaufelchen"(coregonus dispersus) of Lake Constance vary considerably. In many respects, so it seems, they retained the features or characteristics of the primitive" Felchen". This was pointed out in detail elsewhre in our work. It must be mentioned that thisp group does neither possess exceptionally many nor exceptionally few gill-rakers.

Féra	21-28
Palée	22-29
Gravenche	25-33
Bezoule	26-34

by way of comparison:

"Blaufelchen of Lake Constance ♂ 33-42

or: "Sandfelchen" of Lake Constance♂ 19-27
(coregonus fera Jur.)

The "French" coregonus, therefore, with regard to the number of gill-rakers, form intermediary links between the types of the "Blaufelchen" and the Sandfelchen".

With regard to its way of life the "Schwebefelchen" of Lake Geneva appears to be less specialized than the "Blaufelchen". Fatio writes concerning this:(The passage is in the French language .Tr.).

Seeing that the "French" Felchen occasionally come to the shore and again descend into the deep their feed could be more varied than that of the "Blaufelchen", which predominantly inhabits the plankton-region. The stomach contents of the "French" coregonus yield besides plankton-crawfish mostly also insects, worms and molluscs. The "Gravenche" shows itself in its prm primitive form as a small Féra and could dis-

play the same behavior as the "Bondelle" of lake Neuenburger-see, which we can regard as a dwarfed"Palée". We raise the question why Wagler has not dealt with these problems of the Féra-type, which is, perhaps, closest to the primitive"Felchen"; for it is possible that the key for an understanding of the "Felchen"systematics lies therein. It seems that the type of the "French" "Schwebfelchen" did not fit into his scheme.

It becomes evident when we studying the data of the author in detail that also among the remaining "Felchen" that are being dealt with in the work by Wagler, there are several outsiders and typical individuals. A special worry is, for instance, the "Ammerseekilch"(Salmo maraena media Hartm. of lake Ammersee.Tr.). We mention some particulars, according to Wagler, with regard to its special position. In connection with that we compare the "Kilch" of Lake Constance with that of lake Ammersee and refer to our own studies(see Page 62.)

Size of head in %
Lake Constance
Lake Ammersee

Size of head in %
Lake Constance
Lake Ammersee

Size of head in %
Lake Constance
Lake Ammersee

The "Kilch" of the lake Ammersee, with regard to the size of the head, resembles much more certain" Gangfisch", i.e. dwarf "Fechen" than the "Kilch" of Lake Constance. The same can be said for the relative size of the eye:

	Size of eyes in %
Lake Constance	
Lake Ammersee	

	Size of eyes in %
Lake Constance	
Lake Ammersee	

as well as for the height of the caudal peduncle in % with regard to the length of the body:

	Height of caudal peduncle in %
Lake Constance	
Lake Ammersee	

and finally for the number of gill-rakers on the first gill-arch:

	Gill-rakers
Lake Constance	
Lake Ammersee	

I am puzzled why it is still maintained that the "Kleinfelchen"(small "felchen".Tr.) of lake Ammersee is a "Kilch" (Salmo maraena media Hartm. Tr.). The width of the head and the protruding eyes in the pictures by Wagler can be explained by the fact that the fish are afflicted with bloating. We have

observed something like this also with regard to small "Schwebfelchen". On the other hand, we have observed, in the case of "Kilchen"(plural of "Kilch".Tr.) from surface zones, rather narrow heads.

We also must throw a little light upon some of the "Zwangsmassnahmen"(coercive measures. Tr.) advocated by Wagler. It is said on Page 397 of the work of 1937 that the large "Bodenrenken"(bottom-coregonus.Tr.) are mostly "ramsnaesig" (ram-nosed.Tr.), although in many[a] lake(for instance, lake Untersee) it is possible to establish an approach to the 'Blaufelchen" and a terminal mouth can be observed! The "Silberfelchen"(silver-Felchen.Tr.) of lake Untersee, which, according to Wagler, should correspond to the "Sandfelchen", has a "relatively narrow gill-field similar to that of the 'Blaufelchen' ".

It requires ~~rust~~ [much] skill to place the "Felchen" of the foothill Alps in a system, which is established upon the number of the gill-rakers. Also in this case Wagler made some "arrangements", which we can not approve. The "Schwe[b]renke"(some sort of coregonus.Tr.) of lake Chiemsee has less numerous gill-rakers(average below 25), which is rather strange with regard to "Schwebfelchen". The "Blaufelchen" in lake Chiemsee, which Wagler regards as a "Grossschwebefelchen[renke]"(large "Schwebrenke".Tr.) arouses interest, seeing it has an average of 28.6. This is much lower than the total average of the "Blaufelchen(36.3). Would it not be much more simple to regard the "Gangfisch" of lake Chiemsee as a dwarfed "Blaufelchen" of lake Chiemsee? (See also our statements on Page 64.)

As counter-parts we take the two "Schwebfelchen" of lake Vierwaldstaettersee, the large-size "Edelfisch"(coregonus wartmanni nobilis.Tr.) and the small-size"Albeli"(Albula parva.Tr.):

	Gill-rakers	Average
Edelfisch	33-42	37.5
Albeli(according to Wagler)	33-43	39.5
Albeli(according to (Birker, Schweizer and our (own counts)	34-42	38.8
For comparison(total average according (to Wagler):		
"Blaufelchen"		36.3
" Gangfisch"		36.5

Both the large and the small"Schwebfelchen" of lake Vierwaldstaettersee disclose numbers of gill-rakers, which are considerably above the general average. We conclude from that: The small ones derived or originated from the large ones by means of the dwarfing process.

In order to throw light upon the uncertainty of the "arrangements" by Wagler we must cite further instances: He is amazed by the large variation-range in the number of the gill-rakers in the case of the "Felchen" in lakes Zuerichersee and Pfaeffikersee. He admits that"the research had to be done quickly at the expense of accuracy". The "Sandfelchen" were at first numbered among the "Schwebfelchen and then/ " could not be separated anymore clearly". Further:"With regard to lakes Alpsee and Pfaeffikonsee I believed to have recognized, during research, repeatedly the features of the "Sandfelchen". It was impossible to separate the specimens in hand definitely from the typical "Blaufelchen". No wonder that in another place it is said, literally:" The "Blaufelchen" of

of lakes Alpsee, Pfaeffikonsee and Greifensee outwardly approach the "Sandfelchen" very closely, although their growth is the typical growth of the "Blaufelchen". We mention this problem just to show how unreliable the basis of the Wagler systematics is.

The summary on Page 416, which we cite in part, describe best the situation very clearly:

"The gill-rakers can, in general, be of service for the purpose of determining. But they are as unreliable as the features of the body. The development of a single quality of propensity can not be used as a criterion when assigning to one or the other genus; but the conclusion must be based upon the whole. Even at that there would be at times a wrong decision or conclusion made if further helps were not offered in the biology, in general, and in the "Abwachs"(increase?), in particular."

No one will take exception to the fact that I, after such self-criticism by the author of the "four-grade Coregonus-systematics, decline to accept this system. It is not only impractical, but, in my opinion, is not sufficiently undergirded theoretically.

We must still deal with the biological criteria of Wagler upon which much stress is placed by the Bavarian colleague.

The biotope.

The areas inhabited by the main kinds in Lake Constance are well defined and can be well described: The "Kilch" prefers greater depths, the "Sandfelchen" prefers the banks and the slopes of the shore, the "Gangfisch" prefers the open water near the shore- the older age-groups prefer also the greater depths

the "Blaufelchen is a "Hochseefisch"(deep-sea fish.Tr.). Wagler believes that the four"Urfelchen"(primitive "Felchen" Tr.) had already developed this predilection at the time of their arrival in central Europe and that the four can dwell together only in such lakes in which these regions are well-defined and differ properly from one another. If, for instance, the lake is small and of a shallow depth then one or the other, perhaps, two genera can survive alongside one another; but in no case could this be performed by three or four genera. The "Kilch", according to this view, could only get established in Lake Constance and in lake Thunersee. We must raise the question why large lakes such as Lake Geneva, lakes Neuenburgersee, Bielersee and Brienzersee, which are of considerable depth, contain no fish of the "Kilch" kind and why lake Lowerzersee, which is exceptionally shallow contains a "Felchen", which could be, if the Wagler criteria were applied, first of all be assigned to the"Kilch"group. But what about the"Kropfer, i.e. the "Kilch" of lake Thunersee? It is often caught at a depth of 5-10 m, whereas the small "Schwebfelchen", i.e. the "Gangfisch", according to the nomenclature of Wagler in the lake Thunersee stays at a greater depth than the "Kropfer." It would require no skill to muster a dozen objections based upon the fact that Wagler judges everything on the basis of conditions of Lake Constance; for this reason he makes "arrangements"or "generalizations". The variety of the ecological behavior or attitude is, at least, as large as that of the morphological distinguishing features.

FEEDING .

The same applies also to feeding(see also 12, Fasz. 1, Page 149). There are pronounced specialists in some lakes which feed almost exclusively upon Cycladidae and the larvae of Chironomidae and do not change their feeding habits for years. Others again change according to the seasons and undertake distant migrations in order to get to one or the other feeding place. We caught"Felche" in lake Kloentalersee within the region of the brook estuaries, where they fed upon earth worms. It is also known that eggs and hatchlings and even larger fry are devoured; further, an occasional occurrence of monophagy, i.e. specialization upon a single plankton organism, which is picked out with almost unbelievable virtuosity even if it is not dominant in the plankton of that particular season of the year. We must bear in mind that even so-called" Schwebrenken"(some sort of coregonus hovering close to the surface of the water.Tr.) in many lakes often and repeatedly resort to bottom-feed(Lechler, Birrer, Schweizer, Surbeck and others), that at certain seasons of the year, for instance, in Lake Geneva they almost specialize upon mussels and snails and fill the stomach with sand and bottom ooze.

The growth or increase.

I stated my view regarding the uselessness of growth as a criterion for genera quite clearly(see 12, Fasz. 1, Page 152-166). I should like to draw attention to one circumstance:

It was established by means of our breeding experiments that fish of the same vintage, descendants of the same parents, which were raised in one and the same pond can grow differently. The growth is not uniform either in nature or in an experimental pond; it is rather diverse. The uniform size in closed swarms that is to be established later, does not contradict this. When a swarm is being formed there could occur an automatic "sorting", when the large join the large and the small join the small.

Illustr. 65. Route and goal of the spawning "Felchen". An illustration of the variability of an ecological distinguishing mark.

1. Shore. 2 Migrate to the shore(Sandfelchen, Ballen)

3. Schwebfelchen. 4. Spawn in the pelagic(Blaufelchen

5. Into the deep water(Gangfisch, Weissfelchen)

6. Migrate in summer into the deep water(♂ Edelfische)

7. Epilimnion. 8. "Sprungschicht"(leaping layer or stratum?)

9. Hypolimnion.

Spawning habits.

Illustration 65 shows the astounding differences in the spawning habits of individual ecotypes. The behavior of the ecotypes differs nation-wise. Members of one and the same Wagler " genus" disclose often opposite spawning habits.

In all: It is realized that the biological-physiological criteria of Wagler, which he used to differentiate between his"genera" are at least as fluctuating as the morphological criteria.

In these circumstances, so it seems, all we can do is to admit resignedly

that we are not in a position to subdivide the Coregonus race into well-described genera, that, it is true, we have to deal with a group of great variability, that this variability certain is not based upon pure modifications, but often upon genotypical differences, but that the isolation ~~&~~ and consolidation has not yet led to the formation of constant form-types, which could present themselves as "good" genera in the system.

On the question of the re-organization of the "Felchen" system.

1. The reason for a new systematics of the "Felchen".

I discussed this questions with dozens of colleagues: The differential-diagnoses by Fatio and Wagler are altogether unsuitable. No one can, by means of a "determination or classification" table classify a specimen placed before him, without knowing the place where it was found. The old criteria also fail us with regard to entire populations of which we make use in the sense of variations and statistics,.... In order to obtain somewhat valid diagnoses it is necessary to figure out reliable mean values for each age group separately. And even then weha have nothing but disappointment. We meet with transition-links, intermediary forms, which will not fit into our schemes. The only way out is to tear down what has been built up and to start to build anew from the very bottom. This may seem impious. We greatly regret the fact that we are compelled to destroy the great and laborious work of our predecessors; all the more so because we appreciate and respect their diligence and thoroughness. Their mistake, if it can be put that way, lies in the belief that

an entire "Felchen-population can be characterized on the basis of a few specimens without considering, for instance, the great differences in age. Further, we can not spare our predecessors from the rebuke that they, after having studied and described a number of specimens, ~~they~~ yielded to some sort of auto-suggestion and in their minds there consolidated an " ideal" picture, which does not exist in reality. Fatio committed this mistake as well as Wagler and many others. Recently Dottrens committed the same error. What does not fit into the scheme was described, without any further ado, as "not typical" or a "hybrid", perhaps, even eliminated from the calculations and the descriptions. Upon a closer look we can not help but be astonished because these intermediary forms occurred in such large numbers that we must not regard them as exceptions but as the rule.

Let us remember the following: All the "Felchen", in the sense of the zoological system, are to be regarded as members of one uniform or undivided genus. It is unthinkable to split the pikes, the river- or fresh water perches, the brook trouts or, perhaps, the redfin into genera. The same applies to the "Felchen". All these species are polytypical; they differ with regard to color, shape and biological behavior in one body of water from those in another body of water. All of them vary more or less in one and the same body of water.

The systematic categories applied in the new "Felchen" system.

In our new systematics we should have a chance to start from the bottom. It is true that tradition, the contact with the past are valuable in science; but it is also true that we must not be hampered by them. Our thinking must be adjusted to the new level of knowledge.

First of all we point to ~~xhm~~ our general statements on Page 79, where we speak of the genetic principles of evolution. In this place we will deal with the systematic conceptions, which are often used vaguely or misleadingly. This makes a sharp definition a necessity.

The polytypical species.

What is to be conveyed, if I ~~xxx~~ would gather into one genus or species all the hitherto specifically differentiated central European "Felchen?? First of all that all the populations of all the lakes are potentially of an unlimited fecundity among themselves and that the individual or separate varieties(nations and ecotypes) are interlocked to such an extent with one another by means of intermediary forms that a definite separation is hardly plausible. It is assumed that a generalization or uniformity of the systematics will also be carried out in North Germany. We think it possible that at that time the northern "Felchen" will have to be included with those of central Europe in the same "Formenkreis"(circle of forms.Tr.). It seems to me that ~~that~~ it will be possible to include even the Siberian forms. Willer is also inclined to accept this view, seeing that the stated differences are always the distinguishing marks of features of the gill-filter, which vary as much in the nordic forms as in the "Felchen" of the area studied by us:

Holsatus-pidschian-group - broad gill-filter, short rakers

Lavaretus-group - medium-width gill-filter,
-medium-length rakers

Generosus-muksun-group- narrow gill-filter, long rakers.

The nation.

Seeing that we confine ourselves in our monography to Switzerland we only refer to "nations" of the species Coregonus lavaretus, that are indigenous to our land. It will be the privilege of other research workers to add further nations to ours.

As a "nation" I designate a population of a certain part-area of the entire "Verbreitungsgebiet"(distribution-region.Tr.). In our case this means the "Felchen" stocks of a limited lake district, which is included in the upper reaches of an Alpine river. The sketch of our map discloses which areas and nations were considered in our special research. Therefore we differentiate(see Page 116) from SW to NW:

1. Regio rhodanensis(Lake Geneva).
2. Regio jurassica (Jura foothill lakes, Neuenburgersee, (Bielersee and Murtensee).
3. Regio arurensis. Lakes Thunersee and Brienzersee.
4. Regio riurensis. The Reuss lakes: Vierwaldstaettersee, Zugersee, Lowerzersee, Sarnersee and Lungersee.
5. Regio lindimacensis. The Limmat lakes(Zuerichsee and (Walensee.)
6. Regio intermedia. Lakes of the central lakes(Sempachersee, Hallwilersee, Baldeggersee, Greifensee, Pfaeffikersee; further the lower reaches of the river-systems of the Aare, Reuss, Limmat and Rhein rivers where they contain or are inhabited by migratory "Felchen".

7. Regio bodanensis. Lake Constance and lake Untersee.

Illustration 66. Regions of the "Felchen"nations.

If the members of the various nations are compared with one another no/ marked differences, in the morphological sense, are noticed. Especially the varieties, which are possessed of wanderlust, correspond with one another to a large extent. We are of the opinion that the members of this type of "Felchen" are close to the hypothetical primitive"Felchen". It is that form of "Felchen" which arrived in our parts after the glacial period and, at first, "acted" as an anadromous migratory Salmonidae, namely, every year they migrated from the sea to the edge of the Alps and back. Certain peculiarities, which will be described later, support this origin.

In order to separate this variety from others and to name it systematically we are establishing a separate or special ecotype for the migratory "Felchen". This is a category, which in a previous work(1948) we designated as "forma". In the mean time, however, we have realized that this designation is misleading; for it is possible to mean by this designation also season-dimorphous "appearance-forms", etc. We have come to the conclusion to speak of ecotypes and use this category now in our systematics.

The ecotype.

I find it necessary to define clearly here and now the category of the ecotype:

Ecotypes are varieties of a "Formenkreis"(circle of forms.Tr.) which are to be regarded not as "locale-modifications" but as "adaptation"-types that originated through the selection of corresponding"Erbgefuege"(heredity-structures.Tr.).

The ecotypes are actually adapted to their environment. Their peculiarities suit the purpose: The large eye fits the poor light of the deep zone; the slim figure or shape of the "Schwebfelchen" makes this type suitable for ceaseless swimming in the plankton-region. The sub-terminal mouth of the "Bodenfelchen"(bottom-Felchen.Tr.) is suitable for feeding upon bottom-feed. The greater or lesser density of the gill-filter corresponds with the size of the most preferred organisms used as feed. In this sense it seems that the ecotype has actually been adapted to its biotope; its peculiarities are adjusted to the living conditions.

We, however, wish to stress that the purely somatic distinguishing marks gathered from an individual do not constitute the being or substance of the ecotypes. The differentiation is brought about by selection and the changes that interest us are hereditary. This is further supported by the fact that frequently there occur in the swarms of a certain ecotype individuals that have lost their way; for they belong to an entirely different ecotype. We have in mind the "Weissfelchen"(Coregonus lavaretus oekot.primigenius, nat. bodanensis) of Lake Constance, which occur among the "Kilchen"(Salmo maraena media Hartm.) as well as among the "Blaufelchen"(coregonus dispersus.Tr.) and the "Gangfisch"(Albula coerulea.Tr.). Their way or mode of life does not correspond with that of their type, but with that of their fellows in the swarm. Their outward form is not changed or affected by their irregular mode of living; it must be fixed by heredity. It is hard to understand how, for instance, the number of the gill-rakers,

their length and texture could be influenced directly by the "individual" mode of living of a certain specimen. Because of this we must emphasize that the basis of the ecotype is hereditary. We could have produced direct proof of this also by means of separate breeding experiments. We will report elsewhere about this(see Page 162 ff).

Let us now make a list of the ecotypes that occur in the area of our research.

1. Ecotype primigenius.

Distinguishing marks: Intermediary morphological features, pronounced plasticity regarding the mode of living, mixed feed, which changes with the seasons, pronounced wanderlust and a predilaction for moving water even more swiftly flowing water.

We here and now list the forms that belong here and also give their common and systematic names:

1. Regio rhodanensis
   "Féra": Coregonus lavaretus oekot. primigenius, nat. rhodanensis.
2. Regic jurassica
   "Palée": Coregonus lavaretus oekot. primignius, nat. jurassica.
3. Regio intermedia
   "Ballen":Coregonus lavaretus oekot. primigenius, nat. intermedia.
4. Regic arurensis
   "Albock": Coregonus lavaretus oekot. primigenius, nat. arurensis.
5. Regic riusensis
   "Balchen":Coregonus lavaretus oekot. primigenius, nat. riusensis.

7. Regio bodanensis

" Weissfelchen": Coregonus lavaretus oekot. primigenius, nat. bodanensis.

2. Ecotype litoralis.

Distinguishing marks: Sub-terminal oral"slit", blunt head, compressed shape, smaller eyes, short and crude gill-rakers, sparsely placed, covered with a somewhat thicker layer of a soft substance, feeding primarily upon the bottom-feed of the shore zone, stays mostly near the shore, the spawning grounds are close to the shore, spawns in winter.

1. Regio rhodanensis. 2. Regio jurassica. 3. Regio intermedia. 4. Regio arurensis

"Bodenalbock": Coregonus lavaretus oekot. litoralis, nat. arurensis

5. Regio riusensis

"Sandfelchen", "Uferbalchen": Coregonus lavaretus oekot. litoralis, nat. riusensis.

6. Regio lindimacensis

"Bodenblaalig": Coregonus lavaretus oekot. litoralis, nat. lindimacensis.

7. Regio bodanensis

"Sandfelchen": Coregonus lavaretus oekot. litoralis, nat. bodanensis.

3. Ecotype pelagicus.

Distinguishing marks: Terminal mouth, pointed head, slender form, small eyes, numerous, long and delicate gill-rakers, feeding primarily upon plankton, inhabits the pelagic region, spawning habits of various nations differ.

1. Regio rhodanensis

"Lavaret": Coregonus lavaretus oekot. pelagicus, nat. rhodanensis

2. Regio jurassica

3. Regio intermedia

4. Regio arurensis

"Schwebalbock": Coregonus lavaretus oekot. pelagicus, nat. arurensis .

5. Regio riusensis

"Edelfisch": Coregonus lavaretus oekot. pelagicus, nat. riusensis

6. Regio lindimacensis

"Schwebblaalig": Coregonus lavaretus oekot. pelagicus, nat. lindimacensis

7. Regio bodanensis

" Blaufelchen": Coregonus lavaretus oekot. pelagicus, nat. bodanensis.

4. Ecotype profundus

Distinguishing marks: Sub-terminal oral slit or aperture, large eyes, very sparse but also numerous, partly short or also long rather thin gill-rakers, feeds upon bottom-feed and spawn, inhabits the deep, spawns in the deep, protracted spawning season, spawning is early, mostly already in summer.

1. Regio rhodanensis. 2. Regio jurassica- 3. Regio intermedia- 4. Regio arurensis

"Tiefenalbock" or "Kropfer": Coregonus lavaretus oekot. profundus, nat. arurensis.

5. Regio riurensis

"Sommeralbeli": Coregonus lavaretus oekot. profundus, nat. riusensis.

6. Regio lindimacensis

" Tiefenalbeli": Coregonus lavaretus oekot. profundus, nat. lindimacensis

7. Regio bodanensis

"Kilch": Coregonus lavaretus oekot. profundus, nat. bodanensis.

5. Ecotype nanus.

Distinguishing marks: Difference in morphology and biology, mature early, partly already in the first, mostly in the second and even in the third year, large gonads, late poor and very poor growth(dwarfing).

1. Regio rhodanensis

"Gravenche": Coregonus lavaretus oekot. nanus, nat. rhodanensis

2. Regio jurassica

"Bondelle": Coregonus lavaretus oekot. nanus, nat. jurassica

3. Regio intermedia

" Kleinbalden": Coregonus lavaretus oekot. nanus, nat.intermedia.

4. Regio arurensis

" Brienzlig": Coregonus lavaretus oekot. nanus, nat. arurensis

5. Regio riusensis

" Weißfischli": Coregonus lavaretus oekot. nanus, nat.riusensis

6. Regio lindimacensis

" Hegling": Coregonus lavaretus oekot. nanus, nat. lindimacensis

7. Regio bodanensis

"Gangfisch": Coregonus lavaretus oekot. nanus, nat. bodanensis.

Remarks: Seeing that certain features of "nanism" are connected with the particular mode of living in a deep lake the "Profundus" ~~xxxx~~ types may also claim, to a certain extent, the distinguishing marks of the ecotype nanus. On the other hand, however,

the degree of dwarfing differs in ecotype nanus, so that for instance, the "Gravenche"(old style) appears to be less dwarfed than, let us say, the "Brienzlig". It is of interest that various ecotypes in the various regions are inclined to dwarfing; thus the variability of the "nanus"-type is larger than that of the other ecotypes. We point out the supposed origin or descent of the various "Zwergfelchen"(dwarf-Felchen") by means of arrows on our chart.

Illustration 67. A survey of the nations and ecotypes of the Coregonus in Switzerland(Inside circle: Lakes Zuerichsee and Walensee. The chart is self-explanatory.Tr.).

Closing remarks on the systematic part.

It has become clear from our statements that we regard the system as a necessary evil, as an expedient. All the more than 20 varieties, which we have christened or re-christened here, are after all the members of one species. We are fully aware that we with our present-day systematics can not do justice to the variability of tomorrow. Even the fishermen, who, as a rule, are good observers, report time and again the occurrence of"new genera". They make the introduction of "strange blood"from other lakes responsible for the occurrence of unusual colorings, postponements of spawning periods, etc. There is no doubt that the "cultural" measures of man, which caused changes in our waters, brought about interruptions or disturbances. We are thinking here on the eutrophy of the lakes, which,for instance, can become fatal for sooner for the "spawners of the deep" than for the spawners near the shore. Thereby the numerical ratio between the various tribes is changed.

On the other hand, the building up of the shores, the erection of bare walls, the displacement of reed- belts, the artificially created level-fluctuations and run-off regulatings create also new living conditions for the "Felchen" tribes, which have a selective effect upon them and, in the end, will influence, in one way or another, the form-variability of the Coregonus- race. The future systematist will have to take into account all these things. We reiterate: The differentiation is not a historic event, but an actual happening, ~~of process~~.

ECONOMICAL ASPECTS.

Race-breeding(Rassenzucht.).

Although we can not and will not simply dispose of our vulgar or vernacular names for the "Felchen" races of Switzerland, we, nevertheless, as experts must be aware of the fact that all these various "Erscheinungsformen"(appearance-forms. Tr.) always were "fluctuating shapes or forms", that, for instance, even today there occur among the so-called "Gangfische" of Lake Constance various kinds, which, with regard to structure and mode of living, differ from one another. The Fisheries Science(Fischereiwissenschaft) will be interested in selecting those races that are most useful and to improve them through breeding. Let us look at the case of the "Gangfisch" in lake Untersee, which is very instructive for us.

The "Gangfisch" of the past was a small "Zwergfelchen"(dwarf-Felchen. Tr.). About 50 years ago Fatio reported the normal size for fully mature specimens as 23-27 cm.

At times the fish attains a length of 30 cm. At present primarily " Gangfische" of the larger / size are caught in lake Untersee; in recent years we have examined sizable old "Gangfische" of 500 g and more. At any rate, the old "Zwergangfisch"(dwarf-Gangfisch".Tr.) has not at all become extinct. In 1949 we determined a considerable number of fishes, which ranged from 19-22 cm in length; both sexes were fully mature. The females, to some extent, had developed gonads, which constituted, in round figures, 25% of the weight of the body. The majority of these samll fishes was two years old. Among them, however, were those two to four years old, which were slightly larger, but never exceeded the length of 24 cm. These dwarf"Felchen" are not caught with stake nets, but with the "Zuggarn"(Segi)(perhaps-trolling line.Tr.). They are not used for breeding, but are mostly smoke-cured without gutting. The Fisheries Inspection office of Thurgau canton(county)(Adolf Laeubli-deceased- inspector of fisheries) conducted, to a certain extent, race-breeding at Ermatingen, namely, he did not use the dwarfs among the "Gangfische" for artificial breeding. In my opinion it is these measures that are responsible for the increased average weight of"Gangfische" in recent years. Similar methods are applied also in other lakes and there are prospects for success.

The size of the meshes.

It was suggested to enlarge the size of the meshes in the hope to increase thereby the stock of the "Felchen", to save the young "Felchen".

They should be given the chance to spawn one or twice under natural conditions, to say the least. Such protective measures can be applied everywhere, and should be recommended most warmly, where only large-size "Felchen" occur or such races that have not attained full maturity in the first spawning year. This means that they can not be used for artificial breeding until their second spawning- year. This may apply to several or various lakes in Bavaria; but it applies also to several lakes in Switzerland. The situation is altogether different in bodies of water, where, besides the normal-size race, there also occur dwarfed kinds. If in such circumstances , in general, the narrow-mesh net is prohibited or outlawed, a dangerous negative selection is obtained: The large-size fishes are caught and the dwarfed ones are spared. Seeing that, we had to confirm this repeatedly, the dwarfed "Felchen" are often distinguished by exceptional fecundity, they will soon gain the upper hand, will compete with the large-size fishes and drive them out much in the same way as weeds crowd out useful plants. In such cases it is recommended to use nets with fine-meshes; especially during the spawning season of the dwarfs. During this period the young fishes of the large-size fishes, which will also be caught in these nets, are at a distance from the spawning grounds of the dwarfs and thus they are not endangered. Without any hesitation this " catching of spawners to regulate the stock" can be recommended; for thereby the useful race is being protected and preferred. The latter is to be caught with large-mesh nets in a planned " catching of spawners to obtain breeding material" If the hatching is carried out according to modern methods and the rearing, if need be, of early summer hatchlings is undertaken the best results will be obtained.

We have already scored successes in this direction in several lakes in Switzerland. The "Felchen" of lakes Sarnersee, Thunersee and Hallwilersee have been improved in this manner. The commercially useless dwarf-"Felchen" of lakes Thunersee and Brienzersee have been decimated or pushed back in the course of time. The larger growth or size of the "Gangfisch" of lake Untersee-as mentioned above- has been achieved by measures that aim at favoring the large-size form. In lake Alpnachersee the local dwarf form is practically extinct and is being replaced by a good-growing or thrifty "Schwebform"(perhaps-basking form.Tr.). Thus the yield of this part of the lake was considerably increased. In lake Sempachersee there lived formerly a small "Felchen"-race, which was of little economic value, that was replaced by the planned stocking of Gottfried HOFER, a fisherman and fish-culturist. It is likely that in the course of time similar measures will have to be applied to other lakes. Of course, this will only be advisable in the case where there is real competition for feed between the large-size and small-size races. If the kinds inhabit different biotopes- as for instance the "Bodenalbock(Kropfer) of lake Thunersee and the "Kilch" of Lake Constance, which never interfere with the rights of the "Schwebfelchen" of their lakes, then different measures will be applied.

We are of the opinion that no members of a "Felchen"-race should be caught until the respective fishes have attained to their first spawning maturity. The width of the nets, especial-

ly of the "Schwebnetze"(perhaps: floating or suspended net.Tr.), will ~~to~~ have to be adjusted accordingly. In this respect we actively support the efforts of the German colleagues, especially those of Wagler. It can even happen that a certain race, in the first instance, passes through a spawning period of insufficient production and attains its full capacity only at the second maturity. In such cases the first-spawners will have to be spared. However, this is not a general rule. We must emphasize that each lake has its own particular problems and we must warn not to attempt~~s~~ to operate according to a general scheme. What is useful and good in one place has been proven to be a failure in another.

Intensity of fishing out.

The large lakes of our land, at the moment, can be fished out in a rather restricted way. The measures taken by the fisheries authorities are far from extracting the maximum of the yield and often that which is caught in the net of the fishermen represents only a part of the stock large enough for catching. This view is opposed to the view of many colleagues, who believe that, at least,the "Felchen " stocks are fully fished out by the use of nets, even excessively fished out. I am ready to share this view in the case of small lakes that are being fished intensively. However, where, as for instance in Lake Constance, fishing is primarily for "Blaufelchen" with some consequence, there can be no talk of making full use of it. The same applies to Lake Geneva where little fishing is done with stake nets and "Bodennetze" (perhaps: bottom or ground nets. Tr.). Thus the " Gravenche" plays only a subordinate rôle in the resulting catch.

If the yield per hectare of lake is figured out we will marvel time and again that some small lakes yield much more than the large ones. The old irrefutable rule maintains itself again: Continued large yields from intensive fishing are only possible when the lakes are intensively stocked.

We must never forget that the older and over-aged age groups prey upon eggs and hatchlings and, therefore, represent very unfavorable economical factors, doubly unfavorable if they display the symptoms of senile degeneration and of sterility due to age. In the summer of 1949 I had a chance to observe the horrifying canibalism of older "Schwebfelchen". Surbeck reports that he had opened the stomachs of "Blaufelchen, which were filled to capacity with the hatchlings of the "Felchen". I have repeatedly proved that the "Kilche" are wicked devourers of eggs or roe. The same applies also to the dwarf"Felchen" of lakes Vierwaldstaettersee and Walensee and, perhaps, is a wide-spread phenomenon. With the types of nets in use now not nearly all the "Boden"and " Uferfelchen" of the proper size are being caught. It must be assumed that, for instance,a large part of the "Kilche" and of the older "Gangfische" of Lake Constance die a natural death without having been made use of by man.

I, therefore, together with WILLER and others, support the view that a closed season for "Felchen" is only justifiable to the extent to which thereby a sufficient number of spawning fish of the respective main age-group- for instance of the three or four-year old group- is left over. It is necessary, above all else,to study thoroughly the growth and

spawning ratios of individual populations on the basis of which the size of the meshes, the minimum measurements and the closed seasons should be established.

The fluctuations and regulations of the stock.

The causes of the stock-fluctuationsp--the periodic and the irregular ones- are often not clear. According to our own observations and notes, which refer in particular to the lakes Hallwilersee, Zugersee and, partly, to the insubrian lakes, the occurrence of an epidemic at times plays a fatal rôle and reduces the yields, which it takes time to re-build. It is to be assumed with certainty that the degree of extent of eutrophy plays a part in this matter. As a rule the "Wasserblueten" (perhaps: water-flaxseed.Tr.) from Oscillatoria rubescens cause sudden and heavy reverses. Here and there the mass-development of perch, "Trueschen"(perhaps: lamprey) or burbot lamper eel. Tr.) and other competitors and enemies have decimated the stocks. The weather, which, at times, if during spawning or hatching there occur storms or cold snaps, can destroy an entire year's vintage, is another dangerous factor.

Besides these true fluctuations we also know of deceptive "stock-fluctuations", which can be traced to unfavorable conditions during fishing and create the illusion of a scarcity of fish, which doesn't exist. The question, whether we in certain ca cases, in order to maintain a sufficient number of spawners for the coming business of hatching, should reduce the summer catches, arises.

We present a Table on Pp. 128/129 and a graph based upon it. The material applies to Lake Contance and was placed at our disposal- this is gratefully acknowledged- by the federal inspection office for forestry, game and fisheries.

almost without an exception the summer months, which yielded large to very large catches of "Felchen", were followed, not as could be expected by poor, but on the contrary, by ~~xxxx~~ good catches of spawners. This can also be proven with regard to other lakes, which is a further proof for our ~~xxxxx~~ thesis that our "Felchen" lakes are not being over-exploited, that even under favorable conditions for catching or fishing a considerable part of the stock escapes. But also in this case we definitely make an exception with regard to the small lakes the stocks of which can actually be fished out to a certain extent. Summer-fishing or catching in such lakes, of course, is to be arranged in such a way, i.e. measures must be taken that summer-catches do not exceed what is economically feasible. Whether this is to be done more effectually by catch-rationing or the introduction of closed-days or by the establishment of sanctuaries or reservations must be decided in each case.

Regarding "closed-times." or seasons.

In general it should be requested that the closed-times or seasons should be arranged in such a way as to coincide with the spawning periods. Better still, the closed-time or season should start somewhat prior to the spawning period and not end until after the spawning period. In the case of "Felchen"races with a short spawning period it will not be hard to follow this postulate. But what if the spawning period lasts for months? We were able to prove that mature dwarf"Felchen" occur in lakes Vierwaldstaeterrsee and Thunersee ~~occur~~ from June into March. There are fishermen, who maintain that the "Albeli" of the deep can be

caught throughout the year in a condition ready for spawning. I examined mature "Felche" at Staad at the beginning of July in 1949 and mature "Gangfische" in the middle of February in 1950 at Ermatingen. The "Edelfisch" of lake Vierwaldstaettersee also spawns over a long period of time. According to our notes the spawning lasts from July till the end of October.

There is no purpose, in such cases, to introduce a few "closed weeks". A tangible preservation must be brought about in some other way, namely, by "exempting" certain spawning grounds or outlawing certain fishing gear. It must be remembered that in the course of decades there have occurred changes as to the time of spawning in our Coregonus-lakes. This is due partly to the fact that the character of the lake has gradually changed, partly to the stocking with "Felchen" that are strangers to the locale, which produce other than the usual reaction-norms. In this connection we think in particular of the Féras of Lake Geneva and the winter-spawning large "Felchen" of lake Alpnachersee, which are gaining ground also in lake Vierwaldstaettersee.

The most important thing is that in every case where it is possible to make use of a "Felchen" race for artificial rearing the obtaining of eggs or spawn is postponed until the procreative activity of the fishes has reached its maximum. This would safeguard or ensure the catching of, primarily or exclusively, of fully mature specimens. We have observed that at the time when spawners are being caught almost everywhere large numbers of "Felchen" find a chance "to entrust"

their eggs or roe to nature; for, inspite of all the efforts, the nets are not always used at the right time and ~~ea~~in the right place.

Care for the eggs and the hatchlings, proper stocking.

This is not the place to give instructions regarding the rearing of "Felchen". Nevertheless, it is one of our tasks to describe the present-day practice and to criticize it. During the past twenty years we have often and in many places had the opportunity to observe the fishermen and fisheries inspectors, who are engaged in rearing "Felchen", at work. Therefore I deem it necessary to recall a few details, which attracted my attention.

The best results were obtained by hatcheries, which followed the following rules:

1. Careful selection of breeders, the elimination of all semi-mature or over-mature and of all sick and inferior specimens.
2. Strict prevention of adding water before the milt is added (" ultra-dry fertilization".)

The days of intense activity in the hatcheries are dangerous, in general; for due to pressure of work care suffers somewhat. Whenever possible the fertilization of the eggs should take place in the hatchery and, if possible, be carried out by the responsible fisheries inspector and not by the fisherman, who has nothing to do with the eggs afterwards. In very cold weather the eggs often suffer also by remaining in the cold "Bisluft"(perhaps: northern air.Tr.). Fertilized eggs must stay long enough but not too long in the basin. 15-30 minutes after the milt has been added- if this is possible-

the eggs should be placed in breeding-jars, if need be, after they have been cooled.

3. The movement of the eggs in the glass must be slow. Jars that are too full are in greater danger and yield, on the average ge, less than those that are not too full.

4. The best temperature for hatching is that at 4 degrees C. Slight fluctuations, as a rule, cause no harm. It is important to know that the larvae or hatchlings that were hatched later possess more vitality than those hatched earlier, that by means of cold water the time of hatching should be postponed or delayed towards spring as much as possible; for this season offers greater security for the development of the hatchlings than late winter.

5. If the newly-hatched larvae are placed in very cold water then their voracity suffers and they die of starvation. Once a certain degree of weakness or feebleness has been reached the hatchlings can not be saved. Even if an abundance of feed is placed before they will perish. It is to be assumed that the same thing happens to hatchlings that were hatched under natural conditions, if the hatching occurred too early. This may account, as mentioned before, for the fact that occasionally almost entire vintages or year groups are missing.

Once the young "Felchen" have learned to feed properly and to fend for themselves it is possible- up to almost 100%, to have them grow into fine ""Soemmerlinge"(perhaps: Summer - lings or yearlings. Tr.), if the necessary conditions are created. The losses in rearing " Soemmerlinge" of "Felchen" are astonishingly small.

6. When placing the hatchlings in a lake it is of advantage to choose a time when the water has begun to warm up. Where this is not feasible it is best to try "Anfuetterung"(perhaps: additional or intensified feeding.Tr.). It is enough, at times, to offer unfiltered lake-water, which was pumped in. In one hatchery we raised, of course, it was a limited number, of "Soemmerlinge", without any additional feed, on lake-water that was being pumped in. It was possible to care for the small fishes for more than two years.

If the principles mentioned here are followed or observed it is possible, at times, to obtain considerable increases in the yield. We shall mention them in the next chapter.

Chart on Page 128.

Catches of "Blaufelchen" in Lakce Constance over a period of 30 years.

(Swiss Statistics)

Year	Annual catches	Catch of spawners	
	Total kg	Number of eggs obtained	Number of fishes caught

Chart on Page 129.

30 years.

Swiss catches of"Blaufelchen" in Lake Constance 1914-1943.

Total catch during the respective year in kg

Number of the ~~CHNGXX~~ spawners caught in December of the same year.

A few data regarding the yield of "Felchen" from Swiss lakes.

It would be tempting to conclude our monography of the Swiss coregonus with a review of the yield from individual lakes and to enquire whether and to what extent the economic conditions in comparison with the days of our fathers have changed, i.e. have worsened or improved.

There is extensive material at our disposal with regard to statistical data. We point, in particular, to the statistics of Lake Constance and lake Neuenburgersee, which, seeing they were obligatory and strictly kept, affords a good review. Much of interest is found in the publications by Surbeck, Mathey-Doret, Vouga and Quartier as well as in those by other officials of the canton.

However, I must admit that, on the basis of definite experiences, I am very skeptically inclined towards multitudinous statistical data. Instead, I will limit myself to a few data, which are of value to me, and will try to describe, in bold lines, what seems of importance to me. I am persuaded that thus we shall arrive at a picture, true to facts, rather than by compiling many details, which, nevertheless, are always incomplete.

What about the legendary abundance of fishing yields in the past?

Some record-catches of the "good old time" have been dragged through literature for decades and have been quoted zealously from time to time, namely, day-catches of "Bondelles in lake Neuenburgersee of 2330 specimens at the beginning of the 19th century, of 6500 specimens of "Albock" in lake Thunersee in

August, 1640, of 45,000 specimens of "Gangfisch" at Constance in the year 1543 (according to Gessner, 1558). We could multiply the number of individual reports. It concerns sensational reports, exceptional cases upon the basis of which it is not possible to come to conclusions regarding the yield from a certain body of water. Seeing that the "Felchen" travel in swarms it is possible that, under favorable conditions, once in a while also a "gigantic" swarm or schools can get into the large seines. Even at present, in the middle of the 20-ieth century, I have learned from reliable fishermen that occasionally more than 1000 "Felchen" were caught in one haul. The fishermen, however, in most cases maintain silence about such an event fearing the envy of their fellow-men.

The famous Table entitled "The yields of 'Balchen' from lake Sempachersee", which embraces the period from the year 1418-1853, must be read and interpreted with caution. It is certain that the following annual yields are amazingly high:

1568	685,200 fishes
1600	894,600 "
1606	840,200 "
1618	773,700 "

Of course, it is not known how large the fishes were. I studied the original reports, which are kept in the archives at Luzern and could not make sense of the extensive accounts. Here and there mention is made of "small 'Balchen' ". Among other things, what was the size of the "Schonmasse" (size of meshes of nets used in "close-season". Tr)? The

"Felchen" were simply caught when they were yearlings, having a length of 9-10 cm; nets with small meshes were used. It is certified that these small fishes were often smoke-cured. In view of the sparse population and the cumbersome means of transportation it would have been impossible to make use of the fishes in any other way. Our list of the catches at Sempach shows clearly that the catches or yield varied from year to year. In the year 1587 only 86,400 fishes were caught, i.e. barely 10% of the record-catch. In 1751 the yield went down to 12,115 specimens, to 1760 and 7079 fishes. Though Walger in 1938, on the basis of the record-yield of the year 1600, arrived at a yield of 7450 kg per square kilometer, it is to be objected that fixing the average weight of a fish at 125 g is entirely arbitrary and, in our view, is much too high and further that already in the 19th century in comparison with the 17th century the number of the fishes caught went down to one sixth.

It is certain that there was little fishing in many lakes in the 19th century, that "Schwebnetze"(perhaps: suspended or floating nets.Tr.) were hardly known at that time. Fishing was done primarily by means of anchored nets and clap or sweep nets and, further, that in many lakes fishing for "Felchen" was carried out almost exclusively during the spawning season and neglected during the rest of the year.

At any rate the thesis regarding the reduction ϕ in the "Felchen" catches, as maintained by Wagler in 1938, rests upon a very insecure foundation.

But if we wish to move upon solid ground then we must base our statements upon statistical figures, upon records of catches and even then it will be necessary to examine the data very thoroughly.

Regarding the increase in the "Felchen" yields since the introduction of catch-statistics.

The following contains the latest information, for which I am grateful to Mr. A. Mathey-Doret, federal fisheries inspector at Bern, and to several canton functionaries.

Yields of "Felchen" from lakes Bielersee and Thunersee during the years 1939-1945.

Reported by the Forestry Management, Division of Fisheries, Game and Nature Preservation.

Year	Lake Bielersee (19-24 fishermen)		Lake Thunersee (10 fishermen)			
			Brienzlig		other "Felchen" races.	
	No. of fish	kg	Fishes	kg	Fishes	kg

It is clear that limits are set for this development. Each body of water has its own power or potential of production under natural conditions and can not be changed essentially. As pointed out by Willer, there is no sense in stocking a body of water with an unlimited number of hatchlings. One must carefully, considering each case separately, apply the measures, which are most suitable to a body of water with certain natural conditions. One must also bear in mind the competitors among fishes. There are reasons to suspect that the "Felchen" stocks of over-populated lakes are much more exposed to epidemic diseases than those of normally populated lakes.

The best results are always obtained where intensive stocking is followed by intensive fishing.

We deem it important to counter-act energetically the entirely unfounded defeatism of many a fisherman. We enjoy today essentially larger total yields from "Felchen" fishing than our forebears fifty years ago. This can be proven by documents and it is a stimulant to continue on the road chosen, even if the goal achieved: A maximal yield by maintaining a harmonious balance between stocking and fishing or catches, appears to be very remote.

In the next chapter we give a few excerpts from the records, which are to support our statements.

Regarding the earlier and the present yields from our "Felchen" lakes and the measures to improve them.

Unfortunately we know little about the earlier "Felchen" yields of many of our lakes. What we know is hardly definite.

Georg LAEUBLI in his very valuable publication " Statistische und technische Darstellung der Fischerei in Bodensee und Untersee"(Statistical and technical presentation of fishing in Lake Constance and lake Untersee.T$_r$.) estimates the catch of "Gangfische" from lake Untersee in the year 1880 at 100,000-200,000 fishes or specimens per year and the same figures is to apply also to the "Blaufelchen" of the entire Lake Constance region.

Seeing that LAEUBLI himself was a fisherman and, no doubt, was well informed about fishing conditions his data may be accurate for that time.

In view of the fact that today we harvest through professional fishermen in Switzerland alone 180,000 kg of "Blaufelchen" it must be said that "Blaufelchen"-fishing is much more profitable today than 70 years ago. The record- year yielded almost 280,000 kg. Accepting 330 g as the average weight we arrive at a number of specimens or fishes, which, for Switzerland alone, amounts to eight times the yield of 1888. Even the catch of 100,000 of "Gangfische" in lake Untersee is by no-means imposing.

Doctor J. SULZER in his "Beitraege zur Statistik der schweizerischen Fischerei"(Contributions to the statistics of fisheries in Switzerland.Tr.) mentions a coregonus-yield of 15,000 kg for lake Zuerichsee in 1880. This includes the "Blaeulinge", the "Albeli" and the other "Felchen. Today we catch around 60,000 kg per year in lake Zuerichsee. The catch has been quadrupled. We know that around the turn of the century the "Felchen" were still an exceptional phenomenon in several lakes and were of no importance in the economical sense and that the same lakes(lakes Sarnersee, Aegerisee, Lungernsee) have rather "respectable " or substantial "Felchen" stocks. We can not take seriously the complaint, which is repeated from time to time regarding the catastrophical regression in pur "Felchen" fishing industry.

Of course, it is a matter for regret that it must be established that "Felchen"lakes, which at one time produced large yields have, due to the increasing contamination of their waters by sewage from communities and industries, entirely lost their character of"Felchen" lakes and today practically yield no "Felchen".

Here we are thinking of lake Murtensee, which in recent years has never attained or produced a yield of 100 kg of Palées, also on lakes Pfaeffikersee, Greifensee and Baldeggersee the "Felchen" of which, so it seems, are near extinction.

The condition of lake Hallwilersee is also poor, although strenuous afforts are put forth to save it. Of late complaints have been voiced with regard to the retrogression or decrease of the "Balchen" in lake Zugersee and about the occasional appearance, in tremendous quantities, of the Burgundian Chlamydomonas this augurs nothing good.

The large or wide fluctuations in yields are of interest. They occur in some lakes, especially in Lake Geneva. This will be mentioned below. The fluctuations could be traced to a large extent to sewage.

First of all a word regarding the reliability of our figures of statistics. The latest material- it seems to me- very reliable statistical material comes from Mr. Mathey-Doret, federal fisheries inspector, and was placed at my disposal. This is gratefully acknowledged. This material is based upon the official statistics regarding catches. Mr. Mathey-Doret has accurate figures for certain years, which disclose or deal with the delivery of "Felc hen" to wholesale dealers. Thus indirectly the value of the figures given by the fishermen can be checked. We now present the Table, which was composed by Mr. Mathey-Doret personally(see Page 137).

If we intend to use these statistical results in the obtaining of which great caution was applied, we must also be mindful of the errors that are inevitably concealed in our figures.

In most cases the catches of sport-fishermen are not entered in the official lists, seeing that the Sport-fischer fishermen are not compelled to report their catches. This has very little effect upon some lakes. Upon others, on the other hand, the effect is greater than imagined. Here and there anglers have come up with new methods for catching "Felchen". I know of lakes where fishing for "Felchen" is done with ground or bottom hooks and with "floating" lines". Of most importance, however, is the "Hegenen" or "Zupfangeln"(perhaps: jigging.Tr.) at the summer feeding groundse of the "Felchen".

The "Albeckler" of lake Thunersee, an enthusiastic category of anglers for "Felchen" afforded me a look into their records of catches. When the fishing was good some anglers caught 100 and more "Felchen" per day. Confirmed is a day's catch of 520 fish by an angler in the vicinity of Spiez.

Similar figures or numbers were reported by the fishermen of lake Vierwaldstaettersee. The "Hegener"(perhaps; engaged in jigging.Tr.), which are active there, are also passionate "Felchen" anglers. In the year 1942 there were issued in the region of Luzern 300 licences to anglers. For the years 1937 and 1938 I have accurate data:

Year	Number of "Felchen" caught by anglers	Weight

At the moment there are in all about 450 "bootberechtigte" (entitled or permitted to use a boat.Tr.) sport-anglers active on lake Zugersee, who, in most cases, fail to report their catches.

A list, which was provided for me by the authorities in January of 1951, discloses that of all the anglers only 64 had reported their catches. These had caught, in all, 149 kg of "Felchen" during the year 1948/49.

Of late the angling sport has been developing on lakes Aegerisee and Kloentalersee, where "Felchen" are being caught in various ways. But the figures regarding the catches are too few and, partly, too uncertain to permit definite conclusions.

Years ago there was formed a guild of "Blaufelchen" anglers also on Lake Constance, who go out in a so-called "Felchenmaschine"("Blaufelchen"machine.Tr.) and in connection with that they make use of the characteristic habit of the "Blaufelchen", namely, to devour young fishes, by offering spoonhooks to the "Blaufelchen". It is said that the catches of the "Felchen" anglers, at times, are rather considerable.

For these reasons the official figures, which are based upon reports received from profeesional fishermen, are certainly too low.

Nevertheless, they will be compared with the statistics of other lands:

A comparison of the yields from "Felchen" fishing per hectare in the Swiss, Bavarian and the North German lakes.

It is seen that the average yield in Switzerland is considerably larger than in Bavaria:

Country	Area of lake	Year	Yield of "Felchen" in kg	in kg/ha
Bavaria				
Switzerland				

According to A. WILLER the Coregonus lakes in North Germany are classified as follows:

Poor "Felchen" lakes	0.25 to 2.5	kg/ha
Medium " "	2.5 to 5	kg/ha
Good " "	5 to 10	kg/ha
Very good " "	10 kg/ha and more.	

The ratio of the yield to the quantity or density of the stocks.

If many fisheries biologists reach conclusions regarding the quantity or density of the stocks on the basis of figures on the yields this, no doubt, often leads to serious erroneous conclusions.

The fishing in our "Felchen" lakes, at most in a few, I am sure, has been intensified to such an extent that it represents a maximum use of them. In Lake Constance, for instance, the rather substantial "Kilch"stocks are fished only by the few "bottom or ground-net" fishermen, who confine their activities to certain months, when catching is an easy matter. The rewarding catching of "Blaufelchen" by means of the "Klusgarn" (perhaps: hawse-yarn.Tr.) has replaced or pushed all the other methods into the background. It is very important for the figures regarding catches whether the fisherman can sell his catch. If the demand is light then he does not go out fishing for days and weeks; especially if he engages in agriculture besides fishing. Fishing activities increase in times of heavy demand. In lakes where fishing is done more by groups or on a partnership basis, the "Felchen" catches of which are not sold by the individual fisherman but by marketing or selling organisations measures must be enacted to stop the delivery of fish by fits and starts(limited catches and "lake" holidays). This also will effect the results.

Finally, the weather is also a significant factor, which affects the quantity of the catch. I am- in opposition to Walger- of the opinion that the catch, to a very large extent, depends on the weather, the wind and cold snaps or spells, etc. I have witnesses and figures to support this supposition. During the very good fishing season in the summer of 1949 there set in suddenly, in the early part of August, a cold spell, which greatly reduced the catches in various lakes.

I refer here only to the Table on Page 134 and reiterate the statistics of the "Felchen"catches from lakes Bielersee and Thunersee of the years 1939 to 1945, which show the increased demand caused by the war as well as the decrease of fish-consumption by the public xx seeing that meat had again become available.

Justifying the catching of spawner"Felchen", which has been decried xx from time to time as useless.

The planned restoration of the "Felchen" stock in Lake Geneva.

Partly by its own rearing, partly by obtaining hatchlings from other lakes Lake Geneva, which was greatly depleted around the turn of the century with regard to Coregonus gradually once again became a Coregonus lake.

Here are few figures taken from the works of F. Porchet and S. Combe.

Period	Stocking with hatchlings	Origin of hatchlings.
		Lake Geneva
		Lake Geneva
		Lakes Neuenburgersee, Zugersee, Constance
		Lake Neuenburgersee & Lake Geneva
		Lake Geneva.

In % of the total hatchlings released from 1903-1946 (210 millions) the break-down, with regard to proveniences, is as follows:

Original Gravenches and Féras of Lake Geneva 2,27%

"Blaufelchen" of Lake Constance and "Balchen" from lake Zugersee 1.1%

Palées from lake Neuenburgersee 8.74%

New(?)Gravenches of Lake Geneva(1932-1946) 87.76%

The following increases in yield have occurred according to information obtained from statistics.

The catches of "Felchen" in % to the total catch are:

1921 and years following 2%

The retrogression since 1944 has been traced to a heavy increase in the number of perch.

In the mean time there came better times to be followed be a renewed retrogression.

1947 ..... 30.7%

It is interesting to note that the 13% of the part of the Coregonus of 1948- absolute calculation- constitute a much larger amount than the 27% of the year 1943; for they weighed only 49,897 kg. It is possible to recognize at a glance at the statistics of the catches of perch that it is this kind of fish which is "progressing"rapidly in Lake Geneva and threatens again to upset the equilibrium. The authorities observe this development with some apprehension. The fisheries experts, in particular, of canton Waadt fear that the rank increase in the perch stock will make the efforts, begun so auspiciously, for the furtherance of the Salmonidae, especially the rearing of

"Soemmerlinge"(Literally: summerling; perhaps fish hatched in summer.Tr.)at the drinking water pumping station of the city of Lauzanne in Lutry, illusory.

Successful exploitation of "Felchen" in other lakes.

There are other waters, beside Lake Geneva, which have developed in the course of the last decades, due to consequent stocking, into very productive or heavy-yielding "Felchen"lakes. Prior to that the catches of "Felchen" in them was insignificant.

At the turn of the century "Felchen" were known in lake Sarnersee only as an oddity. By means of consequent stocking the yield at present has increased to about 13 kg/ha.

The same applies to lake Lungernsee in which "Felchen" were observed for the first time in 1890. It is only in recent years that the lake has been intensively exploited. It is possible that the fishing was intensified too much. For the period from 1938-1945 the yield amounted to 24.1 kg/ha, which is a record-yield.

But first and foremost it is due to consequent stocking that such fine "Felchen" stocks were developed in the insubrian lakes. They represent a rather important factor in the fishing industry of Tessin canton. The part of the "Felchen" in the total catch today exceeds 30%.

Also in lake Untersee, the hindmost arm of lake Vierwaldstaettersee, the yield of "Felchen" was increased considerably in recent years. The Police Department of canton Uri supplied me with the following records or data:

Year	Kilogramms

Also in this case the upsurge in "Felchen"fishing is due to improved conditions for the rearing of fish.

Improvement of the average weight.

It has been demonstrated in several Swiss waters or lakes that something can be done with regard to quality through the import of "good-growing" "Felchen"races into lakes with unproductive dwarf"Felchen". In this case it was not simply a case of enlarging the size of the meshes in anchored and suspended or floating nets- this was done in Bavaria; for first of all the fast-growing races were introduced and then the size of the meshes was gradually adjusted to the altered conditions(see Page 112).

Lake Sarnersee is a good illustretion of this. The "Felchen" caught in this lake today are of an essentially largere average weight than 20 years ago.

Something similar can be said about lake Alpnachersee the small "Albeli" race of which has become greatly diminished in recent years, whereas, at the same time, a fine "good-growing" "Schwebfelchen"race has come up. This race has increased unexpectedly due to careful rearing or breeding.

All this shows that by constant or consequent care of the stocks by carefulness in catching spawner-"Felchen " and in artificial breeding or rearing good results can be obtained, which prove that the opponents of spawner-"Felchen" catching and of rearing are wrong.

"Felchen" catches in comparison with the total catches from the most important lakes in SWITZERLAND(Year: 1949).

Name of lake	Are in km2	Total yield in kg	Yield per hectare in kg	Portion of "Felchen" in kg	in %	Yield per hectare of "Felchen" in kg	Remarks
Lake Geneva[2]	346.4	334,000	9.6	37,000	11.1	1.1	Sports-fishing only partially covered
Neuenburgersee lake							
Lake Constance							
Lakes							Licenced angling
Vierwaldstaettersee							
Zuerichsee							
Lakes							without licenced angling from the shore
Thunersee							
Langensee							only professional
Bielersee							
Zugersee							only professional
Luganersee							only professional
Brienzersee							
Walensee							only professional without licenced angling.
Murtensee							
All Swiss lakes							
Year 1944/45							

1)Estimate by the federal fisheries inspection office.
2) In the case of not entirely Swiss waters of the border zone the data refer exclusively to the Swiss part of the lakes.

The determination of "Felchen" on the basis of the so-called N-factors according to DOTTRENS.

By

P. STEINMANN and H. AMBUEHL, Aarau.

(Forwarded on Nov. 15, 1950)

E. DOTTRENS, partly alone and partly together with A. QUARTIER- the aim is very commendable- tried to separate the "Felchen" of the southern Swiss waters and those of Savoy as much as possible and thus create a basis for a determination. In later works measurements and counts were made of many specimens of "Felchen". Further, mean values were established and, finally, formulae were evolved for the differentiation-factors, which, so to speak, will permit, as it were, to identify every individual specimen and to name it properly. We examined these formulae and checked our rather extensive material in this respect. In connection with this our attention was attracted by certain phenomena, which call for a close study.

In his most recent work, which deals with the lavaretus des Lac du Bourget, DOTTRENS presents two different N-formulae, namely:

$$N' = \frac{\text{dorsal fin basis}}{\text{anal fin basis}} \text{ plus } = \frac{\text{length of pectoral fin}}{\text{length of dorsal fin}}$$

$$N'' = \frac{\text{dorsal fin basis}}{\text{length of dorsal fin}} \text{ plus } 10 \cdot \frac{\text{length of dorsal fin}}{\text{length of body.}}$$

The figures obtained by means of these formulae are used statistically and graphically.

The measurements thus obtained from the fins play an exceptionally important rôle.

In connection with this it must be observed that it is very difficult to measure the length of the dorsal fin, seeing that this organ is not well-defined at the basis. Therefore, it is inevitable that the compasses are applied at different places and that it is easy to make a mistake in this way. Differences of 1 mm are of great consequence in the formula by Dottrens. Further, the measuring of the pectoral fin is also not an easy matter, seeing that in this case also it is hard to determine where it begins. Due to these technical reasons a wide error-margin is inevitable, which could have an unfavorable effect, in particular upon the N" factor in which to the length of the pectoral fin, expressed in % of the body-length, a tenfold weight is ascribed.

Moreover, the length of the dorsal and pectoral fins is determined to a large extent by age. DOTTRENS, according to his data, considered only adult specimens. What is meant by the term "adult"? We know that "Felchen" continue to grow between spawning periods. Thus it would become necessary to examine separately the various year's growths or vintages, if one were to try to esteblish genetically fixed differences in the length of fins.

The only two figures or numbers, which in our opinion represent actual differentiation-values are the number of the gill-rakers and the number of the scales, which, so it seems, are not affected by age and, therefore, they are valid for the older and younger individuals of a race.

Illustr. 1.(Page 157)

Differentiation between Palées and Bondelles of lake Neuenburgersee.

Ordinates: Number of gill-rakers; abscissae: Number of the scales of lateral lines

Illustr. 2a. (Page 158)

Brienzlig of lake Brienzersee. Presentation on the basis of the N'-factors according to DOTTRENS and the gill-rakers.

Illustr. 2b. Brienzlig of lake Brienzersee. Presentation on the basis of the scales and of the gill-rakers.

Illustr. 3(Page 159) "Felchen" of Lake Constance.

The position of each of the 559 signs is determined by the number of the gill-rakers and the lateral - line scales of the individual in question.

Rectangle in upper right corner

Gangfische
Blaufelchen
Weissfelchen
Sandfelchen
Kilche

We studied how it would be, how this could be presented by a graph if we, instead of using the DOTTRENS factors, would restrict ourselves to scales and gill-rakers. We came to the conclusion that the desired goal can easily be attained by this method. We have presented our own material from lake Neuenburgersee in Illustr. 1. It is evident that in this case, regardless of overlapping, the two races (Bondelles and Palées) can be differentiated just as easy as by the use of the N-factors. Unfortunately our statistic lists of the "Felchen" of lake Neuenburgersee are not very extensive. However, they show sufficiently clearly that our method, as mentioned above, which is based upon distinguishing marks not dependent or affected by age and not prone to errors, brings about the same results.

Seeing that the dimensions or measurements of the fins greatly vary- as is the case with regard to the dwarf-"Felchen" of Lake Brienzersee(Brienzlig)- the concentration of the points of a "Rassenkreises"(race circle. Tr.), desired by DOTTRENS, is not attained and the simple determination by means of scales and gill-rakers is a much safer road to the goal(compare with Illustr. 2).

Illustr. 4. "Felchen"-material of Lake Constance from Illustr. 3, "differa ntiated" according to gill-rakers and scales. The mean values are enclosed by circles; the figure or number indicates what % of the ecotype in question belongs to the circular area indicated or designated.

We have compiled our material, embracing five ecotypes, resulting from our research at Lake Constance, in the graph- Illustration 3. The 559 fishes, that were examined, show an extraordinary variation-range in both directions and cause us to realize that there exists no discontinuity, that everything, so to say, overlaps. Also in this case one could draw a circle around any mean value of an ecotype and thus carry out a certain differentiation. We did that in Illustr. 4. But this method is in no way satisfactory, seeing that it creates an illusion of something, which really does not exist. We must not forget that time and again there occur transitory links between all the ecotypes. In our opinion we must not neglect, as the easiest way out, what does not fit into the scheme.

For the reasons mentioned we must reject the coercive measures by DOTTRENS, though they are interesting as far as they go, to the extent as they might be used as a basis for a general systematics of the "Felchen". The formulae could be of use in the case of differentiating ecotypes of individual lakes, as for instance in the case of the Palées and Bondelles of lake Neuenburgersee. They can also be useful in characterizing and in fixing the limits of two local races of adjoining waters. But what has been differentiated thereby? Definitely not yet any "good genera" in the sense of Linné, but, at most, local varieties or ecotypes of the species Coregonus lavaretus L. The certainty obtained thereby is hardly greater than that of anthropologists, who want to see the Nordic, the Mediterranean, the Alpine and the Dinaric race-circle in the population of Switzerland. In general the results of DOTTRENS confirm the thesis often advanced by us, namely: The polytypical species C.lavaretus contains kinds that differ from one another due to heredity; nevertheless, they are united with one another by means of transitions and intermediary links. The "splitting" of the "polytypical species" has not yet become differentiated to such an extent that we could apply the vulgar or vernacular names used by fishermen to zoological"genera". Everything is still in a state of flux. The formation of genera(German: Artbildung.) is a process occurring now and not a past historical event.

We are convinced that sight of everything would be lost if we were to differentiate, let us say, the entire material on the "Felchen" of Switzerland according to DOTTRENS.

Tables included or enclosed.

In connection with our monography we enclose a few illustrations for the sake of explanation. They refer in particular to our experimental research, which is mentioned in the monography. Tables 1-8. They refer to the "Vergleichszucht"(comparative breeding or rearing. T_r.). Young "Felchen" were reared from the eggs of one pair of Alpnach"Albeli"(early maturing dwarf-"Felchen".) and of one pair of "Féras" from Lake Geneva(late maturing large "Felchen"); the eggs were fertilized on one and the same day and the young "Felchen" were reared under the same conditions. They were cared for until attaining sexual maturity.

A comparative study of this posterity was made from time to time. Samples of this material, which is kept in the museum at Aarau, such as pictures of shapes or forms, of the head-profiles, of the development of the scales and the gill-rakers, are presented in the first 8 Tables.

Table 9: Refers to "hybrid-rearing". A typical female of the large-size " Sandfelchen"race of lake Untersee(Coregonus lavaretus nat. bodanensis, oekot. litoralis) was crossed with a small-size "Gangfisch"male of Cor. lavaretus nat. bodanensis oekot. nanus. The Table makes possible a comparison between the yearling and his brothers and sisters that are a year older.

Tables 10-15: Typical findings in some "Felchen" types, instances of malformations and diseases.

Table 1.

Breeding"Felchen" of the "comparative rearing."

Early development of Féra and Albeli.

Left:(1-4)

Féra

1. just hatched
2. 13 days old, 1.2 cm, 0.01 g.
3. 55 days old, 2.05 cm, 0.07 g.
4. 112 days old, 4.1 cm, 0.52 g.

Right:(a -d) Albeli

a) just hatched
b) 13 days old, 1.9 cm, 0.03 g
c) 55 days old, 2.2 cm, 0.08 g
d) 112 days old, 5.9 cm, 1.6 g.

Table 2.

Breeding "Felchen" of the comparative rearing

From "Soemmerling" (hatchling in summer.Tr.) to yearling.

From top down.

	Age	Length	Weight
Féra	151 days	7.6 cm	3.65 g
Albeli			
Féra			
Albeli			
Féra			
Albeli			

Table 3

Breeding"Felchen" of the comparative breeding .

From yearling to sexually mature"Felchen".

From top down.

	Age.		
Féra	414 days	11.5 cm,	12.8 g
Albeli	414 Days		
Féra	647 days(immature)		

Albeli 647 days(mature male)

Féra 1289 days(mature male)

Féra 1289 days(immature)

Table 4.

Breeding "Felchen" of the comparative rearing(Féra)

The development of the scales.

Age from the day of hatching.

Top row: 86 112 151 180

Second row 205 299 299

(Substitute scale)

Third row: 582 617

Bottom row 617 1289

(inside" Ersatzkern"-nucleus of substitute.)

Table 5

Breeding"Felchen" of the comparative rearing(Albeli)

The development of the scales(2).

Bottom row:"Sandfelchen"- "Gangfisch"- Bastard(hybrid).

Age as of the day of hatching.

Top row: 81 205 299

Middle row: 412 512 617

Bottom row: Left and right e- yearling, right -substitute scale.

Center; Two-year old hybrid.

Table 6.

The gradual formation of the shape of the head.

Breeding "Felchen" of the comparative reering.

(Similarity of Féras and Albeli).

Left: Féra	Right: Albeli
87 days	87 days
205 days	205 days
299 days	299 days

Table 7.

Breeding "Felchen" of the comparative rearing.

The four-year old sexually mature Féra from Lake Geneva, 1289 days old. The ♂ females of the same age were still immature.

Table 8

Breeding"Felchen" of the comparative rearing.

Gradual formation of the gill-rakers.

Left: Féra	Right: Albeli
205 days old, 8.8 cm	87 days old, 5.9 cm.
582 days old, 16.5 cm	412 days old, 12.7 cm
623 days old, 17.2 cm	617 days old, 19.1 cm.

Table 9

Hybrid "Sandfelchen"- "Gangfisch".

(Lake Untersee, Reichenau, 1949)

Left:	Right:
Yearling	Two-year old hybrid
9.9 cm long	19.3 cm long
6.05 g in weight	65 g in weight.

Table 10

Typical heads of "Felchen" from Lake Constance.

(Main races)

Top:	"Sandfelchen"	"Kilch"
Center	"Weissfelchen" (Lake Untersee	"Weissfelchen" (Lake Obersee)
Bottom:	"Blaufelchen"	"Gangfisch".

Table 11.

Samples or instances of gill-rakers on the first gill-arch from "Felchen" races of various nations.

Top row:

"Sandfelchen" "Blaufelchen"

center row:

"Weissfelchen" "Blaufelchen" from lake Chiemsee

bottom:

"Schwebfelchen" of lake Hallstaettersee

Table 12.

Malformations and diseases. I.

Top: "Schwebfelchen" of lake Alpnachersee:

Dorsal fin is missing completely.

Bottom: "Grunder" of lake Walensee:

Abnormally sloping forehead.

Table 13.

Malformations and diseases. II.

Two hermaphrodites from lake Bielersee("Schwebfelchen

Top: Male and female organs fully matured

Bottom: On the one side there is a mature testicle, on th

other side there is a degenerate ovary.

Table 14

Varying growth of scales.

Top: Heavy annual growth with many sclerites The "Kropfer" of lake Thunersee

Bottom: Slight annual growth with few scleriten The "Edelfisch" of lake Vierwaldstaettersee.

Table 15.

Malformations and diseases. III.

Top: Non-parasitic swellung of skin("Melanome") "Blaufelchen".

Center: "Balchen" from lake Zugersee, after removal of skin:

Worm-cysts Triaenophorus crassus, partly opened.

Bottom: "Edelfisch" of lake Vierwaldstaettersee: Swelling of crop and parasitic Copepode: Achtheres pseudobasanistes Neresh.