FISHERY BOARD OF SWEDEN

INSTITUTE OF FRESHWATER RESEARCH

DROTTNINGHOLM

Report No 56

LUND 1977
CARL BLOMS BOKTRYCKERI A.-B.

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Contents

Tagging of Migrating Salmon Smolts (*Salmo salar* L.) in the Vardnes River, Troms, Northern Norway

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I. THE RIVER SYSTEM

The Vardnes river is located on the island of Senja at approximately 69°10'N, 17°30'E, (Fig. 1).

The catchment area is about 16.5 km^2. The average flow is 1 m^3/sec. and in flood up to 16 m^3/sec. In dry periods in summertime this drops to 0.2 m^3/sec. During such periods the water almost disappears in the gravel and stone river bed, especially in the lower parts of the river, and fish cannot ascend from pool to pool. The flow varies greatly with rainfall. In winter time, most of the river bottom is dry, as the precipitation is snow. The river may freeze in October, and the ice usually breaks up by the end of May. During thaw, heavy floods may occur, especially when there is a lot of snow. The location is near the coast and not very cold in winter while summers are usually cold with much rain.

The river flows from the Vardnes lake to the sea and is nearly 2 km long. The bottom is gravel and stones. In the middle reaches is a small fall, Fossen, about 1 m high.

The fish easily ascend this during normal water flow and may enter the lake, about 14 m above sea level. Between the lake and the Fossen fall are two pools and the river area is about 6 da. Below the fall are two smaller pools.

The Vardnes lake is 0.3 km^2 with an average depth of 2—3 m. The bottom is mostly mud with rich vegetation. Into this lake falls the River Trolldalselv, where salmon do not ascend. In Fig. 2 is a map of the water system.

Above Lake Vardnes the catchment area consists mainly of treeless bogs while below the lake the area is forested with birch and a scattering of pines and willows grow along the rivers. Three small farms are situated near the lake but the river is not polluted. The water is almost neutral and an analysis shows the following results:

pH	μmho	mg CaO/l	COD mg O/l	mg NH_4/l	mg Fe/l	mg Zn/l	mg Cu/l
6.70	41.1	6.2	14.1	0.05	0.10	< 0.01	< 0.005

II. THE FISH SPECIES

The most important and common fish is sea trout (*Salmo trutta* L.) which spawns in the rivers both below and above the lake. Sea char (*Salvelinus alpinus* L.) ascend from the sea into the Vardnes lake and spawn there. (A description of the growth is given in MATHISEN and BERG, 1968). Atlantic salmon may ascend to the lake and may even spawn below in the Vardnes river. There are also some stationary trout and char. Sticklebacks (*Gasterosteus aculeatus* L.) are common in the lakes.

III. MATERIAL AND METHODS

A low concrete dam was built on top of the Fossen fall and traps were constructed for catching migrating fish. The descending fish were caught in a WOLF trap (WOLF 1951). The ascending fish had to stop against a screen placed in an opening in the dam. The fish could not stay there for a long time because of the water velocity and would come up to the surface and move backwards. Screens then led them into a pipe and they went down into a trapbox (Fig. 3).

Both traps are in the Fossen fall. Fish migrating to the sea from the river below the fall will not be caught. Salmon smolts in the Vardnes river usually migrate when the highest thaw is over and from 1960, the traps have been very effective.

There was no fishing in the river and in the autumn it was easy to ascertain that all the

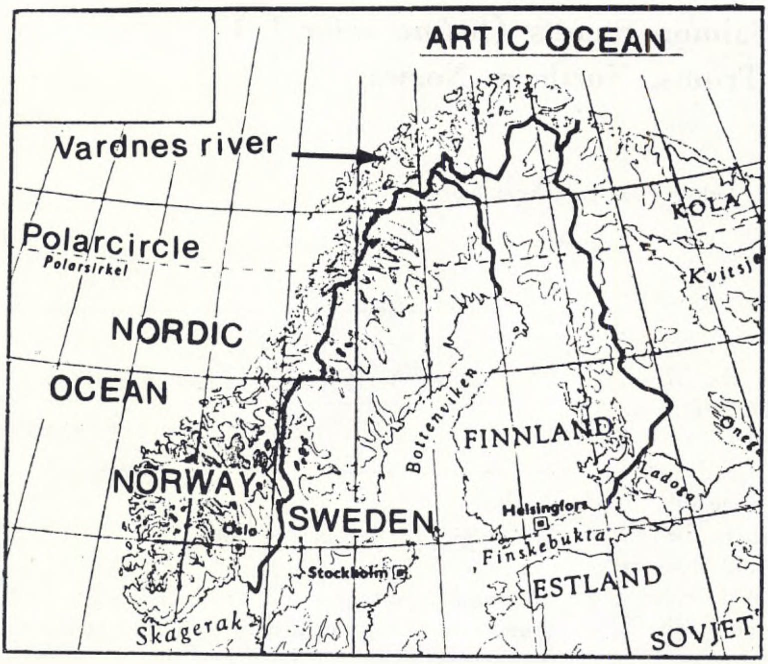

Fig. 1. The location of the Vardnes river.

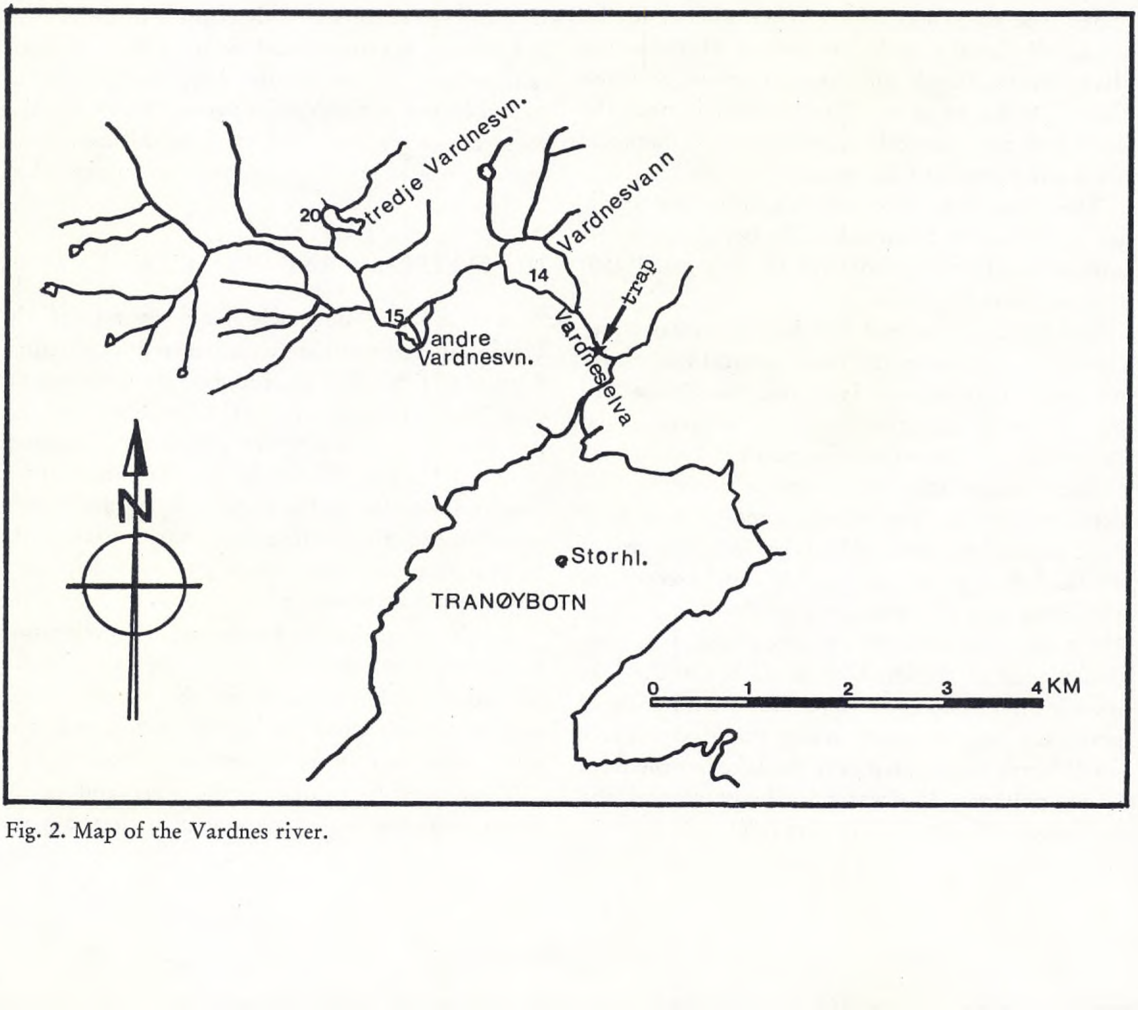

Fig. 2. Map of the Vardnes river.

Table 1. *The number of smolts tagged in Vardnes river and the number recaptured in Vardnes river, in other rivers and in the sea.*

Year	Number tagged	Number recaptured	Number recaptured in V. r.	Number recaptured in other r.	Number recaptured in the sea
1958	1	—	—	—	—
1959	14	1	—	—	1
1960	143	13	—	1	12
1961	35	1	—	—	1
1962	524	20	2	—	18
1963	97	4	—	—	4
1967	116	2	—	2	—
1968	201	22	2	2	18
1969	130	18	1	2	15
1970	123	2	—	—	2
	1384	83	5	7	71

salmon above the fall had passed through the trap.

The traps were used during the years 1958—63 and 1967—70. Migrating fish were captured, anaesthetized, usually with MS 222, tagged with CARLIN tags (CARLIN 1955) and the length measured. Some of the smolts were weighed before they were released. When the smolts migrate from the Vardnes river, they are 11—17 cm in length (BERG 1968).

IV. RESULTS

The number of smolts tagged and the number recaptured are given in Table 1.

All fishing in the Vardnes river was prohibited. The recaptures there were made in the trap. Usually 2—6 spawning salmon were observed in the river. Of the 78 recaptures reported outside the Vardnes river, 71 fish or 91 % were caught in the sea, 7 fish or 9 % in rivers other than the Vardnes river.

During tagging the salmon smolts were treated differently. Some were tagged and measured for length while others were also weighed. In Table 2 the two groups are compared.

The migrating smolts which were weighed had to be handled more than those which were only tagged and the length measured. When handled, they easily lose some scales and get scratched.

Table 2. *Comparison between smolts tagged and length measured and smolts tagged, and weighed.*

Year	Number tagged, not weighed	Number recaptured	% recaptured	Number tagged, and weighed	Number recaptured	% recaptured
1960	66	9	13.6	67	4	6
1961	—	—	—	35	1	3
1962	110	14	12.7	414	6	1.5
1963	38	3	7.9	59	1	1.7
1967	—	—	—	116	2	1.7
1968	101	18	17.8	100	4	4
1969	130	18	13.8	—	—	—
1970	—	—	—	123	2	1.6
Total	445	62	13.9	914	20	2.2

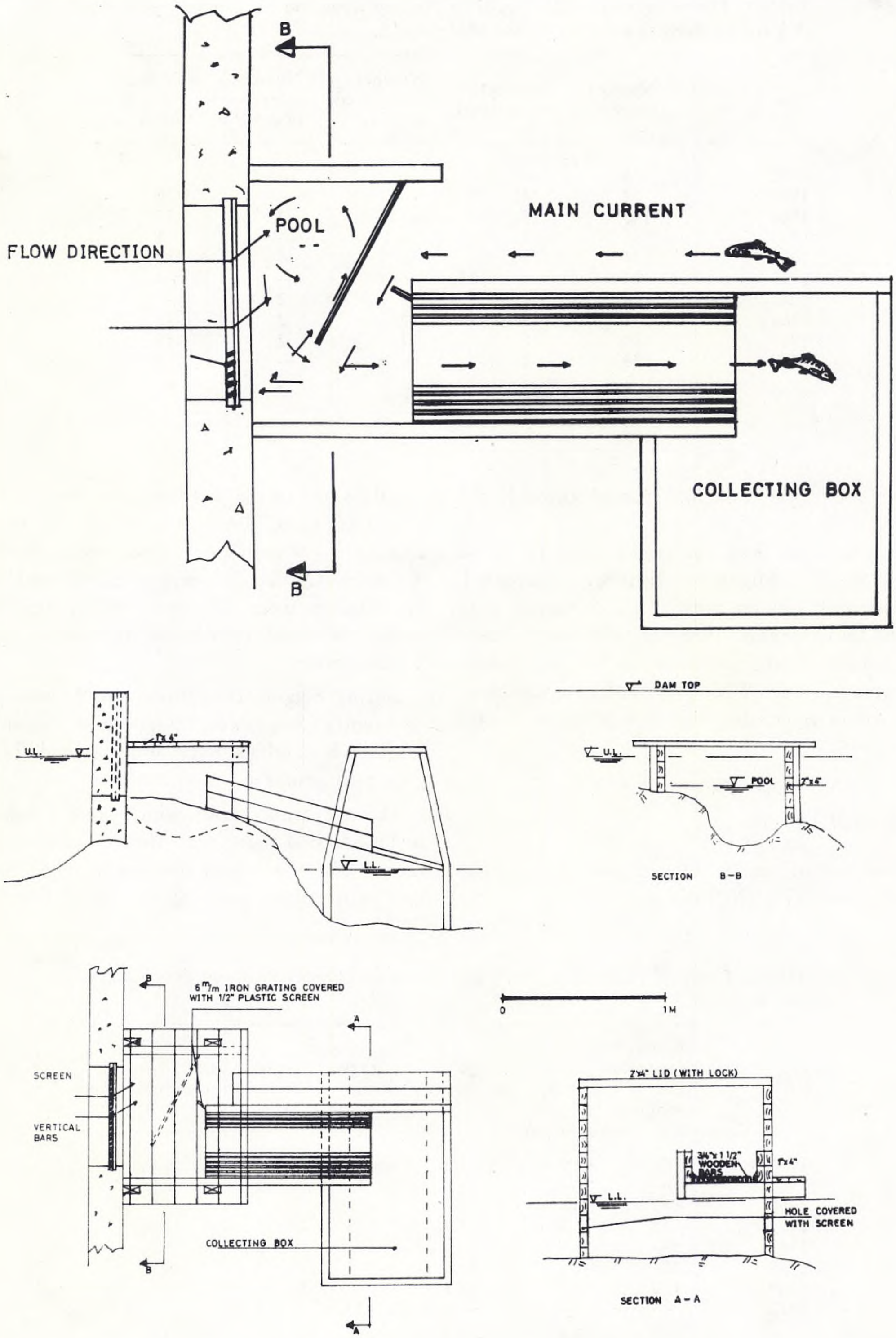

Fig. 3. The trap for ascending fish.

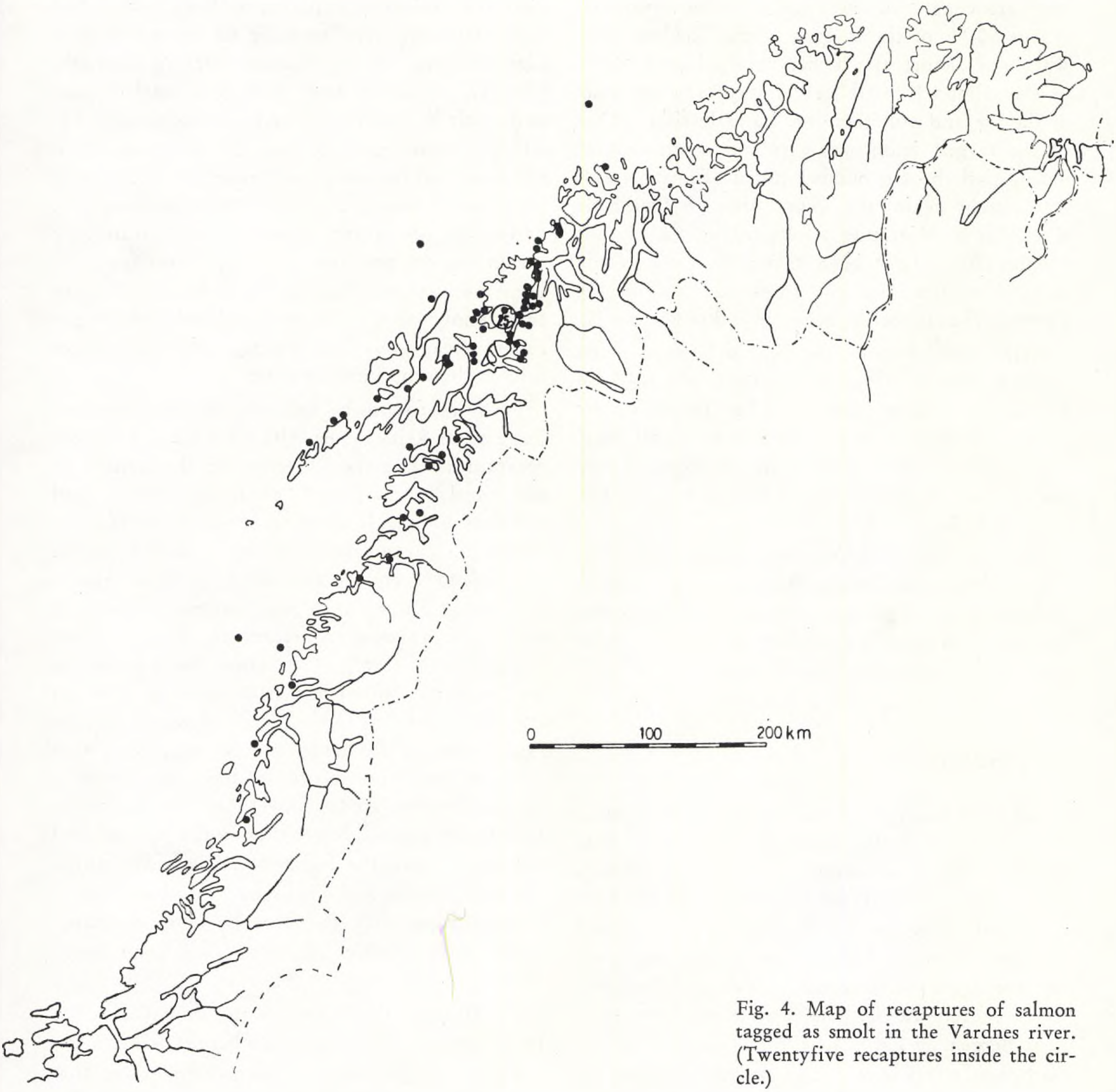

Fig. 4. Map of recaptures of salmon tagged as smolt in the Vardnes river. (Twentyfive recaptures inside the circle.)

Scale samples were never taken from the fish. Those which were weighed gave a recapture of 2.2 %, while those tagged only, gave 13.9 %. The difference between these two groups is highly significant.

Most of the recaptures in the sea were made near the mouth of the Vardnes river. The recaptures were scattered and mostly southwards, as far as Helgeland. Some were caught in the Lofoten and Salten area and a few in the open sea. The recaptures indicate that smolts from the Vardnes river migrate south-west in the sea, and many of them grow up to salmon in the open sea outside Lofoten and Vesterålen Islands. In this area immature salmon have been fished since the middle of the 1960's. Mainly salmon in their second sea-year are caught in the fishery of the open sea. About 60 % of the tagging in the Vardnes river was done before this fishery started and 90 % of the salmon from this river stay only one year in the sea and will therefore be little fished. One of the tagged smolt was captured north-west of Træna and the tag number noted. The same fish was caught again, the second time in Laukhelle river, Senja. Migrating smolts in the sea are not caught. Some have been taken by gulls in the river downstream of the traps and also in the estuary. The number is, however, unknown.

After one year in the sea, a salmon from Vardnes river is 1.2—2.5 kg, after two years 3—4 kg, and after three years 4—5 kg. This is a slow sea-growth such as is found in many small Norwegian salmon rivers. Both males and females may mature and return to the river after only one year in the sea.

The first year in which the traps operated well was in 1960. Since then, the annual smolt production in the Vardnes river has been 29 smolts per da. This river is essentially a sea trout river and also has a small stock of salmon.

V. DISCUSSION

When wild smolts have been tagged with Carlin tags in Norway the recaptures have been low, usually 1—5 %, according to Rosseland (1966). He maintains that if the number of fish reaching the adult stage in the River Sandvikselva had not been greater than the recaptures indicated, the river would have been almost empty of salmon, which indeed was not the case. In the Lone river near Bergen he got a recapture figure of 12 %. Both these rivers have a stock of small salmon, but only Lone has as small fish as the Vardnes river.

Taggings of salmon parr (Berg unpubl.) in northern Norway have given recaptures of adult salmon of 0.7—2.1 %. But the parr can remain at least one winter in the river before migrating and the mortality there is unknown. In 1960 an experiment to transfer smolt into seawater of 34 ‰ salinity was made in Bodø. Of these, two smolts with small lesions in the skin died. Four male smolts which were maturing the same year died also and other experiments have shown that such males are very sensitive to sea water with high salinities. In the Komag river in Finmark, Hagala (1976) in 1946 and 1947 marked parr and smolt by cutting the end off the maxilla. He had the opportunity to check all recaptures from the river and the sea district near the river. From 334 marked young, 55 adult salmon were caught, or 16.5 % (pers. comm.). Salmon can migrate very far in the sea and the recapture rate must have been much greater because the fishermen did not then know about the marking and could not report recaptures. The Komag river has larger salmon than the Vardnes river.

Many recaptures by fishermen are not reported. Tagging of kelts in the Alta river gave 1/3 more recaptures when the fishermen at the bottom of the fjord were visited personally (Berg and Hagala 1972). In Ireland, Piggins (1976) obtained a recapture figure of more than 9 %. He also found (pers. comm.) that untagged smolts gave about 3 times more adult salmon than tagged smolts. In Sweden, the recapture rates are often high (Carlin 1965). But when the Swedes tag smolts at the Norwegian Atlantic coast they get the same low recapture rates obtained by the Norwegians while when the Norwegians tag in Sweden they also record as high recaptures as do the Swedes (Rosseland 1966). In the Baltic, the salinity is much lower than in the Atlantic and the strain upon the fish may be less. Mortalities due to predation and disease may also be different. Small injuries may therefore be more disastrous in the high salinities of the Atlantic than in the Baltic.

In Norway, the fishery in the sea takes such a large proportion of the number of salmon returning for spawning in their home river that in some rivers only the smallest possible number necessary to maintain a stock is left. If the Vardnes river had been fished, the catch of only very few salmon would have ruined the stock.

Seven fish, or 9 % of the recaptures were reported from other rivers. Salmon from very small, temporarily dry rivers may ascend other rivers with more water flow to spawn there. This was also found to be the case in Snøfjord in Finnmark (Berg 1967).

VI. SUMMARY

From 914 smolts measured, weighed and tagged with CARLIN's tag, the adult recaptured was 2.2 %. From 445 smolts which were only measured and tagged, the recaptured was 14 %. The handling of the smolt is of vital importance for their survival when the fish migrate to the high salinity of the Atlantic waters. Only 6 % of the adult salmon returned to the small Vardnes river, 9 % to other rivers, while the rest were caught in the sea. The spawning stock may easily be destroyed in a small river like the Vardnes.

The annual smolt production was 29 per 1000 m^2 (da).

VII. ACKNOWLEDGMENTS

Mr. FREDRIK KAMPEVOLL built the traps and tagged the fish. Mr. BJARNE ABRAHAMSEN and Mr. PAUL HAGALA assisted with the work, and the river owners refrained from fishing in the river. Financial support was received from the Agricultural Research Council of Norway. To all of these I am greatly indebted.

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Pink Salmon, *Oncorhynchus gorbuscha* (Walbaum) in Norway

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I. INTRODUCTION

During the years 1933—39, Sovjet fishery biologists tried unsuccessfully to transplant chum salmon (*Oncorhynchus keta*, WALBAUM) into the Atlantic. In 1956, these attempts were resumed, this time with both pink and chum salmon (BERG 1961). Pink salmon have been caught in varying numbers from year to year since 1960. The first time a few pink salmon were caught in Norwegian waters may have been in 1958 (ABRAHAMSEN, pers. comm.). The fishermen did not then know the fish and did not send them in for examination, so the information cannot be confirmed.

The pink salmon may now be considered established in Norway, and a survey of the occurrence, spawning and experiments with farming are given.

II. MATERIAL AND METHODS

Since 1960, information about the occurrence of pink salmon has been collected through local fishery boards, fishermen and fish-buyers. Much of this information has been checked through personal contact during travels. The fishermen often have photographs of their catch, or the fish is kept frozen. It is easy to get information about pink salmon in North Norway, because the species has black spots on the tail and the fish is now well known by the fishermen. Much of the pink is sold and may be seen at the fish-buyers who usually pay less for the pink than for the small Atlantic salmon. In South Norway, stray rainbow trout from fish farms may be mistaken for pink salmon. In this case the information must be checked.

There is no special fishing for pink salmon in Norway, and the fish is taken when fishing for other species such as Atlantic salmon or sea trout. Pink salmon spawning in the rivers is usually easily observed, as both the behaviour and spawning time is different from other species.

III. OBSERVATIONS OF PINK SALMON IN NORWAY

The pink salmon has a two-year cycle i.e. two years elapse from the time eggs are spent until the mature offspring spawn.

In order to determine whether the pink catch in Norway could be the result of the fry planted in the Murmansk and White Sea areas by the Sovjet authorities, the number of fry should be compared with the catch of pink salmon in Norway the following year. The Sovjet fishery biologists S. S. SURKOV and E. J. SURKOVA (1971) have given the number of pink fry stocked in the years 1959—70 (mimeographed), as referred in Table 1.

The pink salmon have come into Norwegian water as a result of the Russian introduction in their rivers. In every year, the largest catch of pink salmon in Norway has been in Eastern Finnmark, and especially in the district near the USSR border. There is no clear connection, however, between the number of fry planted and the Norwegian catch of adult fish in the next year.

IV. PINK SALMON SPAWNING IN NORWEGIAN RIVERS

After the spawning in 1960 in Snøfjord river, fry migrating to the sea were not observed in 1961 (BERG 1961). In the River Bergeby in Varanger, not far from the USSR border, spawning pink salmon were observed at the beginning of September 1960. In the first days of June, 1961,

Table 1. *Sovjet stockings of pink salmon and subsequent records in Norway.*

Year	Fry stockings in millions	Year	Norwegian records
1959	15.3	1960	20—25,000 kg. Reports from more than 40 rivers in North Norway and found over the whole country. A number of spawning pink observed in many rivers in North Norway.
1960	14.4	1961	2—3,000 kg. Spawning in many rivers but not in great numbers. Several caught in Svalbard. (GULLESTAD 1970.)
1961	10.4	1962	4 reports only.
1962	34.5	1963	About 30 fish reported.
1963	23.7	1964	About 10 reported.
1964	35.9	1965	At least 20,000 kg. Numerous in almost all rivers in Eastern Finnmark. 2 caught in Svalbard. (GULLESTAD 1970.)
1965	None	1966	Found southwards to Trøndelag. Very few, only 5 reports.
1966	None	1967	Very few, about 30 reports, few from rivers.
1967	None	1968	No reports.
1968	5.0	1969	5 reports from Varanger, Finnmark.
1969	8.0	1970	Few reports.
1970	7.0	1971	20—25,000 kg. About the same as in 1960, but more concentrated in Eastern Finnmark. Hundreds caught in rivers. 1 caught in Svalbard. (GULLESTAD 1973.)
1971	?	1972	Some reports from Varanger, some caught in rivers.
1972	?	1973	Better than in 1960. Spawning in rivers as far southwards as in Trøndelag. Numerous in some rivers in Eastern Finnmark.
1973	None?	1974	Not numerous, spawners observed in several rivers especially in Eastern Finnmark.
1974	None?	1975	The run as in 1960. Spawning observed in many rivers, especially in Finnmark.
1975	None?	1976	A number in Finnmark, and some spawners in the rivers there. Single specimens observed in the sea and rivers as far south as Mandal.

BJARNE ABRAHAMSEN, who is a trained observer, saw pink fry migrating to the sea.

In 1975, many pink salmon spawned in the rivers Neiden and Komag in Varanger. Here, fisheries officer VILHELM BJERKNES caught migrating pink fry in June, 1976 (BJERKNES 1977). The pink salmon thus propagate in Norwegian rivers, and parts of the sea stock may belong to certain rivers. Such rivers are Neiden and Tana. The reason why the pink ascend so many different rivers, may be due to the fact that the homing instinct may not work as well in the new surroundings in the Atlantic as in the natural habitat in the Pacific.

In every year since 1960 when a high number of pink were caught in Norwegian coastal waters, spawning pink have been observed in many Norwegian rivers.

V. NET-PEN CULTURE OF PINK SALMON IN NORWAY

The first time pink salmon were cultured in Norway was in 1963. The firm "Hardanger-laks" imported 100,000 eyed-ova from the University of Washington, USA. The hatching went well, but the temperature was low, and many fry were lost. The fish were moved into seawater, started to feed, but were lost by the end of August because of a serious attack of vibriosis. The fish had grown rapidly, and it is a pity they were not given treatment early enough, so that the loss could have been reduced.

By the end of August 1973, ova from pink salmon caught in the Neiden river in Finnmark were fertilized and put into a hatchery in Pasvik.

The diameter of the ova was 6 mm, and in the middle of November, eyed-ova were sent to southern Norway and distributed to three different hatcheries. Of these, a batch of 6120 ova were sent to the Fish Breeding Experimental Station (Forsøksstasjon for fisk), Sunndalsøra. Hatching was finished in November, and only 40 dead ova were registered. On December 21, the fry were split in two groups and put into feeding troughs, one half kept in freshwater and one half put directly into brackish water with 15 ‰ salinity,

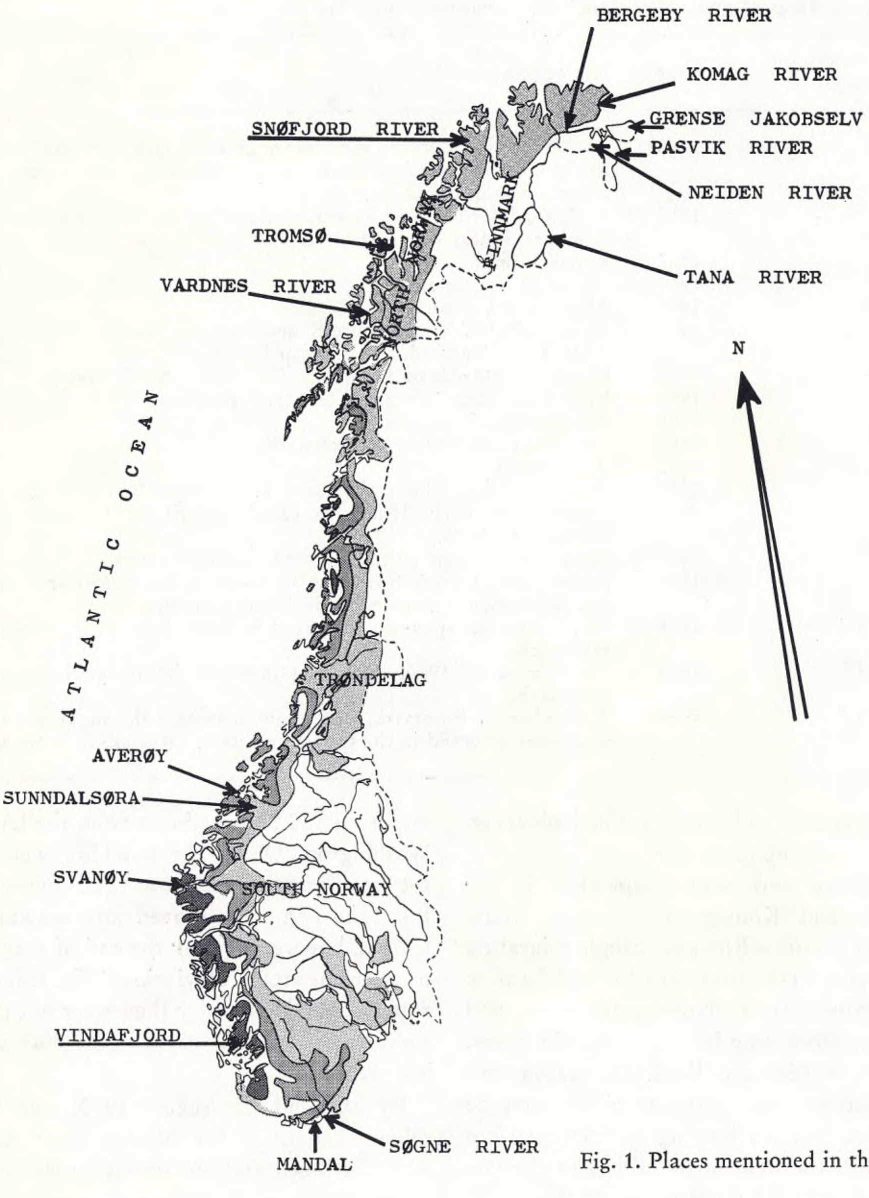

Fig. 1. Places mentioned in the text.

later increased to 23 ‰. The freshwater temperature was kept at 7°C — later raised to 12°C in the freshwater, a little lower in brackish water and the feeding started on dry pellets. The fish went in shoals, took the food easily and grew well and the mortality was only 2.5 % until January 1974. The growth was slower and the mortality higher in brackish water, which had a lower temperature than the freshwater.

Apart from the fact that the water supply to one of the troughs stopped and some fish were killed, the mortality was low and the fish grew well during the winter time.

In the first days of May, all the fish were moved into brackish water and gradually into seawater with 32 ‰ salinity. On June 5, 2000 fish with a mean weight of 35 g were moved into net-pens in the sea at the Research Station at Averøy on the west coast of Norway.

The fish in the sea were first fed with a

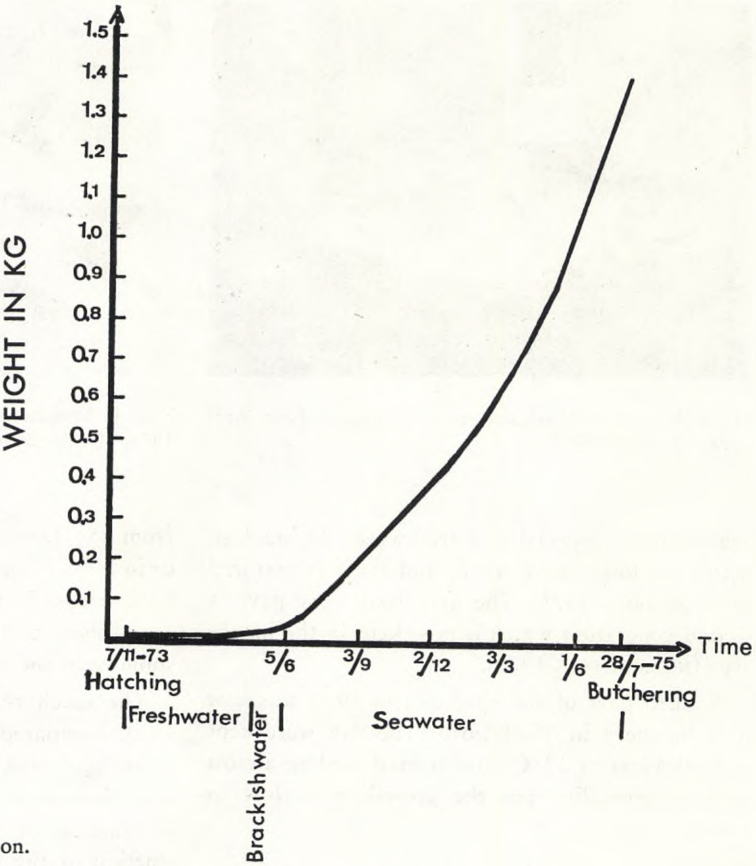

Fig. 2. The growth of reared pink salmon.

mixture of dry and wet food, later with wet food, a mixture of capelin (*Mallotus villosus* MÜLLER, 1776) and binding meal. In June—July 1975, some waste of prawns were mixed into it.

The growth was very good as seen in Fig. 2. On December 1, the mean weight was 400 g, and in August, 1975, the mean weight was 2.1 kg. Most of the fish were then mature. Some were killed for consumption before maturing, and the quality was exellent.

The registered mortality during the sea period was 32.6 % and presented an unexplained loss of 9.8 %. In June, 1975, a serious attack of vibriosis killed 270 fish.

On November 2, 1974, only 12 months after hatching, some of the males were mature and died. The weight of two of them was 300 g and 385 g respectively. Small maturing males have been found in the rivers in Finnmark too (Fig. 3).

Some of the pink salmon did not mature in 1975. On August 10, 1976, 37 were kept alive and examined. All were females, and 16 died the day afterwards. Of these, 3 had spawned in 1975, but the new eggs did not develop normally. Of the 21 fish left, one matured. It was impossible to get seed, and the ova died. In January, 1977, 8 fish were still alive. Pink salmon may therefore have more than a two-year cycle.

The ova fertilised in 1975 gave a few hundred fish, but the mortality was heavy, probably due to unsuitable diet.

About 60 pink salmon from Sunndalsøra were kept in a sea-water pen at Svanøy on the west coast. On September 19, 1975, the largest fish was a female, 4.9 kg, and the mean weight was above 3 kg.

Some eyed-ova were sent to the research station "Fisk og forsøk", Matre. The losses were much

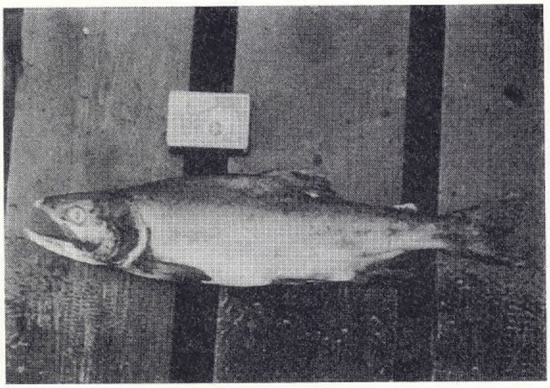

Fig. 3. Mature pink salmon, male, at Averöy Nov. 2nd, 1974, 12 months old.

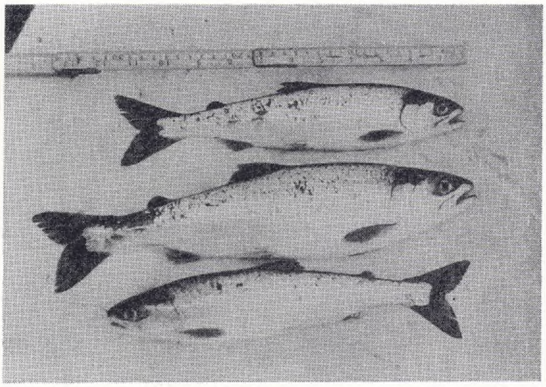

Fig. 4. Immature pink salmon at Averöy Nov. 2nd, 1974, 12 months old.

heavier there, especially in freshwater. In brackish water the losses were small, and the fish matured in September 1975. The fertilized eggs gave a second generation which is now kept in the hatchery (INGEBRIGTSEN 1976).

A third part of the eyed-ova in 1973 was sent to a hatchery in Vindafjord. The fish were kept in freshwater at 12°C, and started feeding almost without mortality but the growth was slow in freshwater.

VI. DISCUSSION

The pink salmon are now well established in North Norway, especially in Finnmark. Further south, only stray fish are observed. In 1976, some pink were caught in south of Norway. They may be stray fish from USSR plantings of pink in the Bay of Riga in the Baltic since 1972. Some 20 pink were caught along the Swedish east coast in 1976 (SVÄRDSON, pers. comm.).

The pink salmon stock of the rivers in Eastern Finnmark may be reproducing itself. In some of the rivers, spawning has been observed every year and the good stocks are fairly dense. Such rivers are River Grense-Jakobselv, River Pasvik, River Neiden, River Komag and River Tana. In other large rivers in the same area there are only a few pinks.

Even if the pink salmon is now established, the stock may again disappear, as it has done from the Dennis river in Maine (RICKER 1954), or in New Foundland (BLAIR 1968, LEAR 1975). In both areas, it looked as if the pink were well established, and spawning was observed, but after some years the stock is dwindling away.

The catch of Atlantic salmon will always be small, compared with what could be expected from a stock of pink salmon. As RICKER (1954) points out, there is a striking contrast between the low production of the Atlantic and the large production of the Pacific salmon species. Norwegian fishermen, emigrating to North America's west coast and fishing for salmon there, have long offered their help in establishing Pacific salmon in Norway. The reason it has not been done, is the fear of disease and competition with the native Atlantic salmon and sea trout. The question has been discussed for more than half a century. Many of the Norwegian salmon rivers are now used for hydro-electric purposes. The estuaries and often the lower parts of the rivers also may remain undisturbed. These areas are not usually suitable for the spawning of Atlantic salmon, but may be used by pink salmon. In the southern districts of Norway, many of the best salmon rivers are now almost devoid of salmon, because of acid water. In such rivers, pink salmon may spawn in the estuary where the influx of sea water will neutralize the acidity. The first small-scale experiment was done in 1976 with 10,000 pink fry which had been fed for some months and planted in the River Søgne. This is the same as "sea ranching" in the Pacific (McNeel and Baily 1975). When it is possible to produce more fry, the experiments will be enlarged.

For the Norwegian fish farmers, the pink salmon may prove a useful fish. They may produce fish for consumption in marine waters from the fry stage to about 400 g in less than one year (Fig. 4). The results are very promising so far, and may be compared with those obtained in Puget Sound (Novotny 1975).

VII. SUMMARY

Sovjet biologists have introduced pink salmon from the Pacific into the Murmansk and White Sea areas. These have spread into Norwegian waters and ascend many Norwegian rivers. It appears as if the homing instinct is not functioning as efficiently as in the natural habitats.

Spawning by pink salmon has been recorded in many Norwegian rivers, and fry migrating to the sea have been observed. The stock in some of the rivers may be self-reproducing.

The pink are caught accidentally during fishing for other species, but there is no special fishing for this species. The catches vary greatly from year to year.

Some pink are farmed, and the first experiment with planting fry has been undertaken. We hope to use pink to establish a new stock of fish in the estuary of acid rivers where the Atlantic salmon are extinct. The pink salmon may be used in fish farming for consumption, and its growth is exellent in the sea. In captivity, some female pink salmon survived spawning, and were still alive a year later. Some females are 3 years old, and have not yet spawned. Some males matured after one summer i.e. 11—12 months after hatching. All the others died after maturing, 18—20 months after hatching.

VIII. ACKNOWLEDGMENTS

I am particularly indebted to Dr H. Skjervold, Mr A. Kittelsen and Mr K. Gunnes at the Fish Breeding Experimental Station, Sunndalsøra, and Mr H. Kaldheim, Ilsvåg Bruk, Vindafjord for information about pink farming, fishery assistants B. Abrahamsen and P. Hagala for their help, Mr N. Gullestad for information about pink in Svalbard, and fisheries officer V. Bjerknes about migrating pink fry. Dr E. O. Salo at the University of Washington and Dr A. V. Novotny at the Northwest Fisheries Center, Washington furnished information on the rearing pink in the Pacific. Fisheries research officer K. W. Jensen has given advice about the manuscript. Financial support was received from the Agricultural Research Council of Norway.

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On the Dynamics and Exploitation of the Population of Brown Trout, *Salmo trutta* L., in Lake Øvre Heimdalsvatn, Southern Norway

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CONTENTS

INTRODUCTION

In the more than 300,000 lakes and tarns that are found on Norwegian maps, the brown trout is the most common fish species. In tens of thousands of these water bodies the brown trout is the single fish species present. For Norway a scientifically sound basis for the management of trout lakes is therefore of more than academic interest.

Knut Dahl realized this, and his paper on trout populations (Dahl 1917) provided a sound foundation for further work. However, the tedious task of analysing huge materials of trout scales, and perhaps also respect for the mathematics involved, have prevented nearly all the later Norwegian fresh water biologists from serious studies of the dynamics of trout populations. One of the exceptions was I. D. Sømme whose main results concerning Norwegian trout populations are found in Sømme (1941).

The impressive post-war advances in the statistical methods used in population dynamics and the rapidly increasing availability of computers, render studies of this kind more promising and easier than in Dahl's and Sømme's time. The Ministry of Agriculture's purchase of a mountain area including a trout lake (Øvre Heimdalsvatn) that could be used solely for controlled experiments gave the author an opportunity to study a trout population's reactions on exploitation.

Since 1958 all fishing in the lake has been completely controlled and poaching efficiently prevented. In the years until 1968 only the fish population could be studied. From the autumn 1968 the Norwegian P. F. section of the International Biological Programme laid their project to Ø. Heimdalsvatn. This gave staff and facilities to expand the studies in the lake to production at different trophic levels. The scope of this paper, however, is limited to the trout population and its exploitation.

An isolated population of a single species of easily aged individuals gives a good basis for enquiries into some of the methods and models used in fish population dynamics. The main aim has been to see if such models can predict reasonably accurate trout yields and in that way be useful for the management of trout fisheries.

SYMBOLS

The symbols used are mainly those listed in IBP Handbook No. 3. In statistics the terminology used by SNEDECOR (1959) has been followed.

—	A bar over a symbol indicates a mean value.
⌒	A circumflex over a symbol indicates an estimate.
A	Total mortality rate $(A=1-S)$.
a	Y-axis intercept in certain linear regressions.
B	Biomass of a population or an age-group.
b	Slope in certain linear regressions.
c	Number of fish in a sample examined for tags or marks.
D	Population density (biomass in kg divided by lake area in hectares).
F	1. Instantaneous coefficient of fishing mortality. 2. Variance ratio, used in analysis of variance (»anova»).
f	Fishing effort.
G	Coefficient of growth in weight, exponential model.
K	Coefficient of growth in length in the simple VON BERTALANFFY growth model.
l	Total length of a fish in cm.
l_m	Modal length.
l_n	Length of a fish at the time an annulus is formed on the scales.
L_∞	Asymptotic length in the simple VON BERTALANFFY growth model.
M	Instantaneous coefficient of natural mortality.
m	Number of fish tagged or marked.
N	1. Number of fish in population or other defined group. 2. Number of observations (in tables).
P	1. Production. 2. Probability.
q	Catchability coefficient $(q=F/f)$.
R	Coefficient of multiple correlation.
r	1. Number of recaptured tagged or marked fish in a sample. 2. Coefficient of correlation.
S	Survival rate.
s	Oral radius of a fish scale.
S.E.	Standard error.
t_0	A parameter in the simple VON BERTALANFFY growth model.
var	Variance.
w	Weight of an individual fish (in g).
Y	Yield from a fish stock (in kg).
Z	Instantaneous coefficient of total mortality $(Z=F+M)$.
φ	Mesh size in mm (knot to nearest knot).

I. THE LAKE AND ITS CATCHMENT AREA

Lake Øvre Heimdalsvatn is located at an altitude of 1090 m in the central mountain area of Southern Norway (61°25′N, 8°43′E). The lake area is 0.775 km², the maximum depth 13 m and the mean depth 4.7 m. The lake is usually ice covered from medio October to primo June.

The catchment area is 24 km². The rock north of the lake is gabbro and south of the lake gneiss. In the west is a smaller area of Precambrian-Eocambrian sedimentaries.

The lake water is poor in electrolytes, with conductivity (K_{18}) 10—30. In spite of the low Ca content pH is usually about 6.5.

The brown trout is the major fish species in the lake. In 1969 the minnow (*Phoxinus phoxinus*, L.) was observed for the first time. During the years of this study the minnow population was negligible.

The most important food animals were *Gammarus lacustris*, *Lepidurus arcticus* and insect larvae, especially of *Chironomidae* and *Trichoptera*. Fish were not observed in the trout stomachs.

The trout spawns in September—October in the outlet river and in one of the biggest of the inlet brooks. Especially in the outlet the spawning and breeding conditions are excellent.

II. MATERIALS AND METHODS

Table 1 shows for each of the years 1958—72 the number and weight of all trout removed from the lake, catch per unit of fishing effort, total fishing effort and the number of scale samples that were analysed.

In all years gill-nets were the main fishing gear, and only a small fraction of the catch was taken on other kinds of gear. All fishing effort was therefore converted to gill-net effort.

The catchability of trout on gill nets is very dependent on the weather, the time of the year, the type of thread used, the mesh size etc. Therefore the uncorrected number of gill-net nights used during the year is a poor measure of the effective fishing effort.

Nets made of platil (monofilament) and of nylon twine were used. On average platil nets caught 44 % more trout than nylon nets of the same mesh size. Platil-net effort were therefore converted to nylon-net efforts by multiplying the number of platil-net nights by 1.44.

In September 1966 the nets were on seven occasions lifted and moved only every second night. In that month a net that was standing two nights caught on average 2.30 fish while a net that stood one night caught 1.80 fish. The standard fishing effort was corrected accordingly.

Most of the catch was taken by netting in August and the second half of September. For each year the average catch per net per night in August and per net per night in September was calculated. The unweighted mean of these two figures was used as the average catch per unit of effort for that year. The fishing effort in all other months was calculated by dividing the number of fish caught by this average. The resulting figure was added to the number of net-nights actually used in August and in September.

All mesh sizes given are from knot to knot. The usual length of the nets used was 25.1 m and the depth 1.41 m.

In the years 1959—70 a "pilot fleet" of eight platil nets in mesh sizes 24, 26, 28, 30, 32, 34, 36, 38 mm was regularly used.

A specification of all nets used in the different years is given in Table 2.

In the years 1960—63 the same 50 nets were used. In 1964 varying numbers of nets were in use. In 1965 20 nylon twine nets with mesh size 32 mm were included in the fleet and 19 nets with 26 mm mesh left out. During the years 1965—69 the same 50 nets were used, but in addition some fishing was done in 1969 with monofil nets without noting the mesh size used. Also in 1970 monofil nets with un-noted mesh sizes were used in addition to the nets listed in Table 2.

A selectivity curve was used to build up a series of eight nets which in combination have nearly the same efficiency on all trout sizes between 18 and 45 cm. From one to six of these series were used in 1972—73. The series used in 1971 were slightly different as 22 mm nets were used instead of the 26 mm nets.

Table 1 shows the number of scale samples that were analysed each year. Care was taken to obtain samples that were representative of the catch — usually by sampling the whole catch on certain days distributed through the main fishing season. In addition all trout caught on the eight pilot nets were sampled and kept separately. The scale samples were taken in an area near the lateral line between the adipose and the back of the dorsal fin. (DANNEVIG and HØST 1931).

Age determination and growth measurements were done on scale impressions on celluloid. Usually 5—6 impressions were examined for each fish.

I. D. SØMME (1941) was aware that in scales of trout from Norwegian mountain lakes the first, very small annulus was frequently overlooked, and he mentions that this annulus can lie only three — four circuli from the centre of the scale. 40 years' experience with scales of this kind has convinced the present author that very commonly the first winter is not registered as an annulus. The same is known from the highlands in Scotland (FROST and BROWN 1967). In Ø. Heimdalsvatn a very small annulus consisting of two—four narrow circuli is often found close to the centre of the scale. In some cases this first annulus could

Table 1. *Yearly catch, fishing effort and number of scale samples.*

Year	Catch			Av. catch per gill-net night in Aug.—Sept.	Corrected fishing effort (gill-net nights)	No. of scale samples
	No.	Kg	Kg/ha			
1958	2765	470	6.1	2.535	1091	222
1959	1919	343	4.4	1.815	1056	520
1960	2884	559	7.2	2.205	1329	742
1961	2934	561	7.2	1.895	1550	718
1962	1971	375	4.8	1.575	1250	666
1963	2108	403	5.2	1.560	1365	589
1964	2285	456	5.9	1.675	1495	609
1965	1647	384	5.0	1.275	1295	603
1966	1897	445	5.7	1.290	1485	692
1967	1780	415	5.4	1.300	1390	606
1968	1460	350	4.5	1.260	1220	709
1969	981	228	2.9	1.040	1042	880
1970	1172	305	3.9	1.645	719	965
1971	2170	424	5.5	1.940	1119	1369
1972	1954	390	5.0	1.588	1232	1934

only be seen in one or two scales while it was missing in the other scales from the same fish. In some scale samples the first annulus was obviously missing. Some cases were doubtful. After much consideration I chose to add one year to the age of all trout with five or more wide circuli before the first annulus.

Excepting the first annulus the scales were usually easy to read. The summer growth (widely spaced circuli) began usually in June or the first half of July, and the first "winter" circuli were usually appearing in September. To avoid confusion of age groups 1th January was always used as the "birthday".

Tagging began in August 1958. In all later years a number of trout were tagged in June—beginning of July. In the last years some additional tagging was done in September—October. Details are

Table 2. *Specification of the nets used.*

Year	Cotton 20—32 mm	Monofilament (Platil)						Nylon twine										No. of nets used pr. night
		Pilot net	24 mm	26 mm	30 mm	32 mm	36 mm	20 mm	22 mm	26 mm	28 mm	30 mm	32 mm	34 mm	38 mm	43.5 mm	51 mm	
1957	19	6	1	11	3	—	—	—	—	10	—	—	—	—	—	—	—	44—50
1958	3	7	—	10	1	—	—	—	—	10	—	—	—	—	—	—	—	29—31
1959	—	8	—	10	2	—	—	—	—	10	—	10	—	—	—	—	—	40
1960	—	8	—	10	12	—	—	—	—	10	—	10	—	—	—	—	—	50
1961	—	8	—	10	12	—	—	—	—	10	—	10	—	—	—	—	—	50
1962	—	8	—	10	12	—	—	—	—	10	—	10	—	—	—	—	—	50
1963	—	8	—	10	12	—	—	—	—	10	—	10	—	—	—	—	—	50
1964	—	8	1	10	10	—	—	—	—	9	—	10	—	—	—	—	—	41—48
1965	—	8	—	—	11	—	1	—	—	—	—	10	20	—	—	—	—	50
1966	—	8	—	—	11	—	1	—	—	—	—	10	20	—	—	—	—	50
1967	—	8	—	—	12	—	—	—	—	—	—	10	20	—	—	—	—	50
1968	—	8	—	—	12	—	—	—	—	—	—	10	20	—	—	—	—	50
1969	—	8	—	—	12	—	—	—	—	—	—	10	20	—	—	—	—	50
1970	—	8	—	—	3	6	3	—	—	—	—	1	11	—	—	—	—	20—32
1971	—	—	—	—	—	—	—	12	6	—	6	—	—	6	6	6	6	8—48
1972	—	—	—	—	—	—	—	12	—	6	6	—	—	6	6	6	6	8—48
1973	—	—	—	—	—	—	—	12	—	6	6	—	—	6	6	6	6	8—48

shown in Table 18. Fish for tagging were caught on a chase net or on otter or spinner. Usually the fish were kept in confinement over-night for observation. Fish which showed signs of having been damaged by the handling were not used for tagging. The tagging was done under water in a small tub. In 1961—63 anaesthetics were used, but later left off as unnecessary. Numbered CARLIN tags with double steel thread were used. The tags were attached below the front end of the dorsal fin in the way commonly used in smolt tagging (see CARLIN 1955).

III. GILL-NET SELECTIVITY

Gill nets with a fixed mesh size catch trout in a wide range of length, but with highest efficiency for trout of a certain length, the modal length 1_m.

BARANOV was the first worker who successfully tackled the problem of gill-net selectivity. He found already in 1913 for Caspian herring that the modal lengths of fish caught in gill nets were proportional to the mesh sizes. He also assumed that nets with different mesh sizes would fish with equal efficiency on fish of their modal lengths. Further, as a working hypothesis he assumed that a net's efficiency to catch fish of varying sizes could be described by the normal probability curve with the modal length as the mean. A short review of BARANOV's and other early authors' contributions is given by Mc COMBIE and FRY (1960).

An important step was taken by HOLT (1957) who accepted BARANOV's results and in addition assumed that the standard deviation would be the same for the selectivity curves for two adjacent mesh sizes. If these assumptions are correct, selectivity curves can be constructed by the method described by HOLT.

For a person with long experience in gill-netting for trout BARANOV's and HOLT's hypothesis that the symmetric normal curve will describe net selectivity is unacceptable. If trout only, or nearly only, were caught by one mesh of the net entangled around the fish just in front of the dorsal a symmetric curve could be expected to describe the efficiency of the gear in relation to trout size. However, trout that are too big for a certain mesh size are very commonly caught on a single mesh fastened far in front of the dorsal but very seldom, if ever, behind the dorsal. A trout that is a little smaller than the modal length will therefore have a better chance to pass through than a trout that is a little bigger than the modal length. This could be expected to give a positive skew to curves describing gill-net efficiency in relation to trout length. Furthermore, trout are often entangled in other ways: By the gillcover, by the tips of the maxillae, by the teeth and by the hook on the lower jaw. Very small trout are frequently caught by biting over a thread and "sewing" this through mesh after mesh so in the end the fish is entangled as in a trammel net. Events of this kind can be expected to result in unsymmetric selection curves.

Skew models for selectivity curves have also been applied. OLSEN (1959) modified HOLT's model by not specifying the exponential function in advance. His selection curves for herring gill nets were slightly skewed.

REGIER and ROBSON (1966) re-examined five previously described methods for estimating gill-net selection and introduced and examined four more. The models were used on whitefish and the best results were obtained from a skew-normal model.

While OLSEN's model gave satisfactory results for his herring material, the same model gave striking differences to the skew-normal model when used on whitefish (Fig. 4 in REGIER and ROBSON, 1966).

As any kind of mathematic model chosen in advance will influence the shape of the derived selection curve, the author prefers as far as possible to avoid postulated models and use the graphical method as demonstrated by GULLAND and HARDING (1961).

It has been shown for many fish species that the girth (greatest circumference) is proportional, or nearly proportional to the total length. Fig. 1 shows a plot of 343 trout lengths and the corresponding girths measured at the front of the dorsal. The fish were caught in the lake in August 1970 and August 1971 and measured shortly after capture. The predictive regression line is:

$$\text{Girth (mm)} = \div 10.03 \text{ mm} + 0.5417 \cdot \text{l (mm)}. \quad (1)$$

There is a strong correlation ($r = 0.98$) of girth on total length.

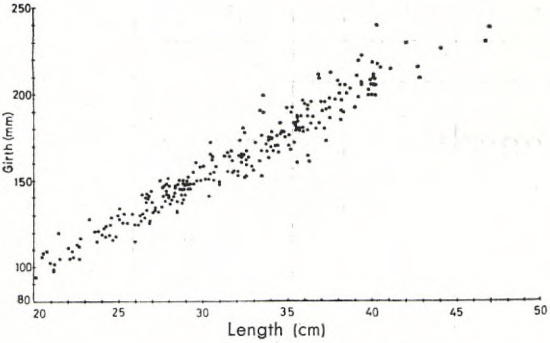

Fig. 1. Relation between girth and total length in 343 trout.

The linear relation described by equation (1) is so near to proportionality that we also for trout can expect the modal length to be very nearly proportional to the mesh size.

The material used for selectivity estimates consisted of 1223 trout caught on the pilot nets during 87 nights in 1964—69. Every net was used on every night concerned. Of the 8 pilot nets the 34 mm net was left out because it was shorter than the others. Because of the scarcity of big trout in the population few fish were caught on the 38 mm net, and this net was also excluded. The smallest mesh, 24 mm, will most efficiently catch trout with lengths about 230 mm. Trout that were smaller than 22 cm were excluded because they were outside the most efficient range of any of the nets used.

Plots of the most efficiently caught fish lengths against the corresponding mesh size gave $l_m = 9.6\ \varphi$ where l_m is the modal length and φ the mesh size (knot to knot).

The first step in the computations according to GULLAND-HARDING's method is shown in Table 3. The estimated efficiency was plotted against the fraction best mesh/mesh used and a smooth curve drawn by eye through the points (Fig. 2). This curve was used to obtain a better estimate of the nets' pooled efficiency for each cm-group of fish. The pooled number of fish within each cm-group was then divided by the estimated pooled efficiency to obtain a new and better estimate of the relative abundance of the number of fish within each cm-group. The new abundance estimates were in turn used to obtain new estimates of the efficiency of each mesh size for each fish length and a new curve was drawn by eye. As only insignificant changes were obtained by continued iteration, this curve was accepted as the best estimate, and the values for relative efficiency transformed to percentages (Fig. 3). As the most efficient mesh is proportional to l_m, the fraction l/l_m is equivalent to GULLAND-HARDING's term Best mesh/mesh used.

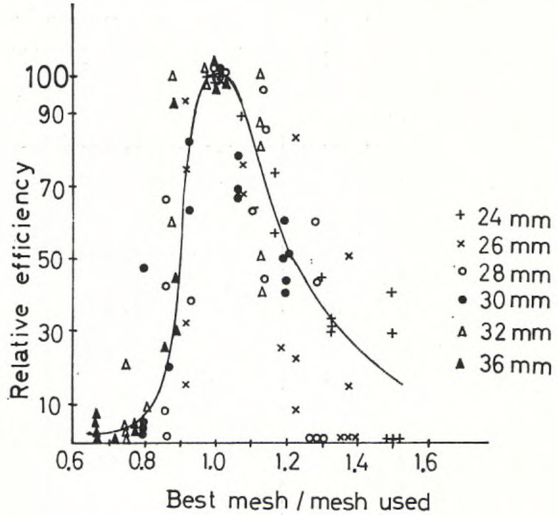

Fig. 2. Gill-net selectivity. (Explanation in the text.)

As expected the selection curve has a pronounced positive skew. There is considerable scatter

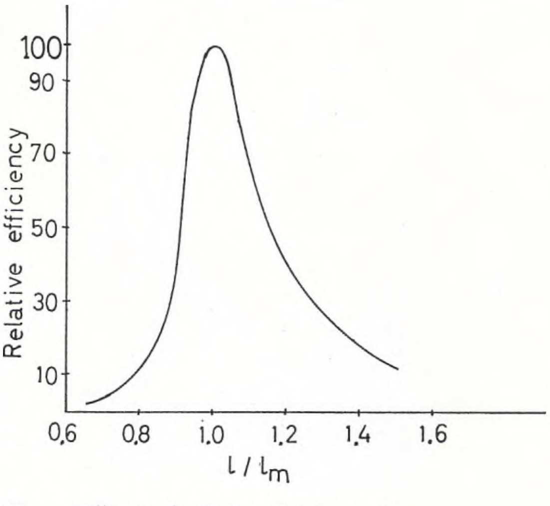

Fig. 3. Gill-net selectivity. (Final curve.)

Table 3. *Gill-net selectivity estimates (Gulland—Harding's method, first step).*

Length (cm)	Max. no. fish	Best mesh (mm)	24 mm			26 mm			28 mm			30 mm			32 mm			36 mm		
			B.m./ Mesh used	No.	Eff.	BM/M	No.	Eff.	BM/M	No.	Eff.	BM/M	No.	Eff.	BM/M	No.	Eff.	BM/M	No.	Eff.
22	71	24	1.0	71	1.0	0.92	11	0.15	0.86	1	0.01	0.80	1	0.01	0.75	3	0.04	0.67	1	0.01
23	66	24	1.0	66	1.0	0.92	21	0.32	0.86	5	0.08	0.80	2	0.03	0.75	0	0	0.67	1	0.02
24	43	24	1.0	43	1.0	0.92	40	0.93	0.86	18	0.42	0.80	2	0.05	0.75	1	0.02	0.67	3	0.07
25	45	26	1.08	40	0.89	1.00	45	1.00	0.93	17	0.38	0.87	9	0.20	0.81	4	0.09	0.72	0	0
26	38	24	1.0	38	1.0	0.92	28	0.74	0.86	25	0.66	0.80	18	0.47	0.75	8	0.21	0.67	2	0.05
27	30	28	1.17	22	0.73	1.08	20	0.67	1.00	30	1.00	0.93	19	0.63	0.88	18	0.60	0.78	1	0.03
28	28	28	1.17	16	0.57	1.08	21	0.75	1.00	28	1.00	0.93	23	0.82	0.88	28	1.00	0.78	1	0.04
29	23	32	1.33	7	0.30	1.23	19	0.83	1.14	22	0.96	1.07	18	0.78	1.00	23	1.00	0.89	7	0.30
30	16	30, 32	1.30	7	0.44	1.19	4	0.25	1.11	10	0.63	1.03	16	1.00	0.97	16	1.00	0.86	4	0.25
31	13	32	1.33	4	0.31	1.23	1	0.08	1.14	11	0.85	1.07	9	0.69	1.00	13	1.00	0.89	12	0.92
32	9	32	1.33	3	0.33	1.23	2	0.22	1.14	4	0.44	1.07	6	0.67	1.00	9	1.00	0.89	4	0.44
33	7	36	1.50	2	0.29	1.38	1	0.14	1.29	3	0.43	1.20	3	0.43	1.13	6	0.86	1.00	7	1.00
34	5	36	1.50	2	0.40	1.38	0	0	1.29	3	0.60	1.20	3	0.60	1.13	2	0.40	1.00	5	1.00
35	5	36	1.50	0	0	1.38	0	0	1.29	0	0	1.20	2	0.40	1.13	4	0.80	1.00	5	1.00
36	2	36	1.50	0	0	1.38	1	0.50	1.29	0	0	1.20	1	0.50	1.13	2	1.00	1.00	2	1.00
37	2	36	1.50	0	0	1.38	0	0	1.29	0	0	1.20	1	0.50	1.13	1	0.50	1.00	2	1.00

Table 4. *Combined selectivity of fleets of gill-nets used in different years.*

Trout length (cm)	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
8 Pilot nets	5	7	11	19	34	46	57	67	73	81	84	92	93	96	100	99	100	96	89	82	72	65	56	50	45	40
50 nets 1960—63	4	5	9	15	26	53	68	78	88	100	98	95	88	75	67	59	54	49	44	40	35	31	28	25	22	19
50 nets 1965—68	2	3	3	5	28	13	19	28	43	69	93	100	100	90	83	69	62	56	50	45	41	37	33	30	26	24
48 nets 1971	77	96	100	85	72	62	60	67	69	64	62	62	67	72	77	82	87	86	85	85	90	88	87	86	83	82
48 nets 1972—74	76	84	77	62	60	76	83	95	95	83	79	77	82	86	91	95	100	98	95	94	99	95	94	92	89	88

of the points, especially on the right side of the mode, and for abscissa values of more than about 1.20 the position of the curve is very uncertain.

The length distribution of 2274 trout taken 1965—69 on 30 mm and 32 mm gill nets of nylon twine indicated for this kind of thread the relation $l_m = 9.4\ \varphi$. A new trial with seven different meshes of nylon twine in August—September 1971 gave $l_m = 9.42\ \varphi$. As sufficient data is not available for computing selection curves for nylon twine nets, we shall assume that the general selection curve for nets of nylon twine has the same form as that found for the monofilament nets, and that only the l_m-values are different for the two kinds of nets. The selectivity of the pilot nets alone and of the combined fleets of nets (including the pilot nets) used from 1960 is shown in Table 4. In 1957—59 and in 1964 no accurate registration was made. The combined fleet used in 1960—63 was fishing most efficiently on trout with lengths 27—29 cm and in 1965—68 on trout with lengths 28—31 cm. For trout smaller than the most vulnerable length the fleet's efficiency is declining rather steeply. The fleets used from 1971 fish more evenly on all the trout lengths listed in the table.

IV. MIGRATION, MOVEMENTS, DISPERSAL

As most of the trout samples from our lake were caught in stationary gear (gill-nets) that could only catch moving fish, our conclusions can easily be biased if certain biological groups of trout have patterns of movement or dispersal that differ strongly from other groups.

The first question to answer is whether the trout population in Ø. Heimdalsvatn can be regarded as a discrete population. Data from some other Norwegian mountain lakes have shown that trout to a considerable extent can move from lake to lake (see for instance I. D. Sømme 1936, 1941, Jensen 1963). Especially on Hardangervidda big lakes seem to share the trout population with the surrounding smaller lakes and tarns, and migrations from lake to tarn and *vice versa* are very common.

The 2.5 km long river from our lake down to the big Lake Nedre Heimdalsvatn has no waterfall that the trout could not ascend. However, excepting the spawning periods, only small trout are found in the river except occasionally a stray bigger specimen on the reaches nearest to the lakes.

Of the thousands of trout tagged in Ø. Heimdalsvatn only two have been reported caught in N. Heimdalsvatn. Both these fish were anaesthetized, tagged and released together near the outlet of the upper lake on 1 July 1962, and they were recaptured in the lower lake, near the inlet, three and four days later. The author believes that the combined effects of the drug used and the proximity of the outlet to the point of release is the most probable explanation of the apparently erratic movements of these two specimens.

175 trout caught on a chase net were tagged in N. Heimdalsvatn 21—27 July 1962. Of these 111 were later reported recaptured in N. Heimdalsvatn, and one was caught three years later in Lake Sandvatn which is situated below N. Heimdalsvatn. Not a single specimen was recaptured on the river or in Ø. Heimdalsvatn.

In the summers 1970—72 a weir with traps for ascending and descending trout has been operated in the outlet of Ø. Heimdalsvatn. The catch data give no indication that fish ascend from the lower to the upper lake.

Of the inflowing brooks only one harbours trout. It comes from a tarn (Brurskartjern) with a trout population. The brook is more than 3 km long and the fall about 210 m. Trout from Ø. Heimdalsvatn spawn in the lower reaches of this brook, and fry and fingerling-sized trout are common. For long stretches above the first impassable waterfall the brook seems to be empty of fish. In the summers 1970—72, except during floods, the movements of trout in the lowest end of the brook were controlled by means of a weir and wire-mesh traps. With very few exceptions the fish that descended to the lake were small, young specimens, probably from the lower part of the brook. We can safely conclude that in the exploited age groups eventual emigration to or immigration from other trout populations must be so insignificant that the population belonging to Ø. Heimdalsvatn for all practical purposes can be regarded as a discrete unit. Another history is that at certain periods spawners leave the lake for their spawning places and that the youngest age groups live in the inflowing and outflowing streams near to the lake.

I. D. SØMME (1936, 1941) found in small lakes on Hardangervidda no indication that the individual trout were stationary and stuck to a certain part of the lake. On the contrary, his impression was that the trout moved about so fast and so consistently that he compared the lake to a kind of sporting arena. This is in accordance with the old experience that small, shallow lakes in that area can be fished nearly empty with a surprisingly small gill-net effort. As an example nearly every trout in catchable size was caught by an effort of only 117 gill-net nights in the 90 ha. Lake Flåttatjønn (I. D. SØMME, 1941).

In other lakes in Norway the trout's behaviour can be very different. SØMME (1941) was aware of this and mentions that a small tagging experiment he had undertaken in N. Heimdalsvatn indicated that the trout there were more stationary than in the lakes on Hardangervidda.

In Ø. Heimdalsvatn, which is smaller than Flåttatjønn, a many times higher gill-net effort has induced a much smaller fishing mortality than in Flåttatjönn. Hence the vulnerability of the trout to gill-netting is significantly smaller in Ø. Heimdalsvatn. As the modern nets of nylon twine or monofilament are more efficient than the cotton nets used by SØMME, the solution must be sought in the behaviour of the fish. The simplest and most probable explanation is that in Ø. Heimdalsvatn the nightly movements of the trout on the average cover much shorter distances than in Flåttatjønn. This does not by itself imply that the trout in Ø. Heimdalsvatn are stationary.

BALL and JONES (1962) concluded from 56 recaptures in Llyn Tegid that "the trout showed no tendency to form home areas for any longer than one week". However, as mentioned by THORPE (1974) this conclusion is not warranted by their published data. GUSTAFSON *et al.* (1969) showed "a certain amount of stationariness" for the brown trout in a small mountain lake in Sweden. THORPE (1974) showed that in summer homing to previous feeding areas was characteristic of trout tagged in "favourable" areas of Loch Leven.

As shown by many authors (SCHUCK 1945, ALLEN 1951, STUART 1953, KALLEBERG 1958) in rivers or under simulated river conditions trout are very stationary, stick to their chosen territory and defend this against intruders. Foraging is done in the immediate neighbourhood of the "home". This may be an adaption to lotic conditions where the food is moved to the fish by the current. In a lentic environment more active movements are necessary for foraging, but as we shall see from the tagging experiments, trout can have a strong tendency to keep to a very limited part of the lake for a long time.

Conclusions influenced by the behaviour of tagged or marked fish can be very misleading if catching, handling and tagging or marking seriously affect the subsequent behaviour of the tagged specimens.

Fig. 4 shows recaptures made one year or more after the trout were caught, tagged and released in the area between the broken lines in the eastern part of the lake. Fig. 5 shows recaptures from tagging in an area in the western part of the lake. The black circles indicate recaptures one year or more after tagging, while the crosses show recaptures made in the year of tagging, but at least one month after the tagging took place.
Only fish that were released in the area where they were originally caught have been included.

As indicated by Fig. 5, the dispersal of the recaptures after one year or more is about the same as that found after at least one month but within the year of tagging. There is a pronounced difference in the recaptures from the two tagging areas because most of the recaptures were made in or near the area where the trout was caught and released the first time.

Maps of recaptures in the first month after tagging show the same general picture: Some individuals have moved far away, but most of the recaptures were done in the tagging area.

Trout that have been captured more than twice complete the picture. A few of these were caught on the outlet river during their spawning migration, and these recaptures were omitted. For 93 trout that were caught three times (two recaptures after tagging) both places of recapture were recorded. Of the first-time recapture 51 (55 per cent) were made in the place where the fish was

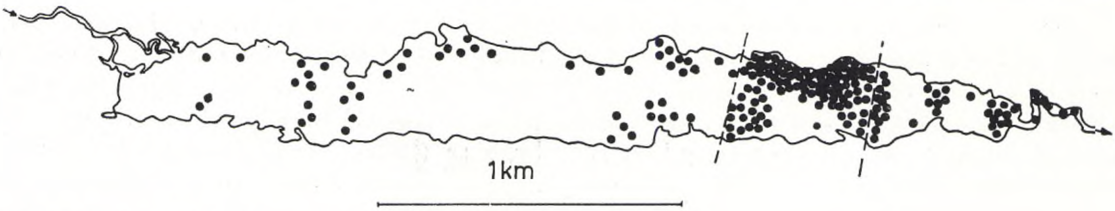

Fig. 4. Recaptures of tagged trout. (Explanation in the text.)

originally caught. Of these 51 fish 25 were caught the third time on the same place while 26 had moved to a new place, but often to a neighbouring area. Of the 42 trout that had moved to a new place between tagging and first recapture 13 (31 per cent) were caught again in this place, 3 specimens had returned to the place where they were originally tagged and 25 (60 per cent) had moved to a third place before they were caught the third time.

For 16 fish the place of capture was registered four times. For 13 (81 per cent) of these the second place of capture was the same as the first. 7 fish (44 per cent) were caught three times on the same place and 2 were caught on the same place all four times. No fish was caught on four different places.

Two fish were captured five times. One of these was caught on the same place in the eastern part of the lake on 3.7. -71, 5.10. -71, 4.7. -72 and 6.7. -72. On 3.9. -72 it was caught in the western part of the lake. The second specimen was caught and tagged on 11.7. -65 near the mouth of a brook on the northern shore of the lake. 13.7. -65 it had crossed over to the southern shore 200 m from the first place, and it was found here again on 8.7. -66. 10.7. -66 it had moved 600 m westwards and crossed the lake again, and on 16.7. -70 it was finally captured 700 m farther west.

Both fishing effort and tagging was in all years distributed as evenly as possible along the lake. Therefore, no significant differences in the dispersal of recaptures from different tagging places could be expected if the fish moved quickly about all over the lake. The probability to catch the same specimen repeatedly in the same place would also be slight. All evidence shows that the trout in this lake has a strong tendency to keep within some small part of the lake for long periods, but there are frequent exceptions from this rule. All recaptures on the upper part of the outlet and probably also some of the other recaptures outside the tagging area, represent fish on their spawning migration which, of course, breaks eventual stationarity. The stationarity may well be more absolute than indicated by the tagged fish. A trout that has been frightened by capture and handling may well be liable to run away, but can hardly be expected to be more stationary than the untagged specimens. Furthermore, trout that move much about will have a higher probability of recapture on the stationary gill nets than fish that move less and may be overrepresented in the catches.

Fortunately, care was taken from the beginning to distribute fishing effort and tagging along the whole lake. Trout that were caught on the chase net were usually set out in or very near to the place where they were caught. Trout caught for

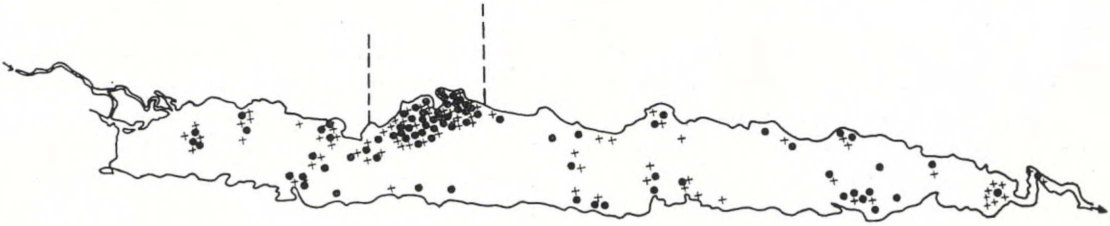

Fig. 5. Recaptures of tagged trout. (Explanation in the text.)

tagging on otter were kept alive in a bucket of water, and 3—5 specimens were often mixed in the bucket before the batch was tagged, so their original places of capture were not known. Therefore fish caught on otter before tagging have not been included in the dispersal studies. There are indications in the material that "displaced" tagged trout have a tendency to return to the area where they were originally caught. If this is so, the practice of transporting all tagged fish to one place (for instance in the middle of the lake) for release, will increase the movements of the tagged fish and the probability of catching them on stationary gear, and the probability of recapture will increase with the distance the homing fish has to cover. As the fishing effort in Ø. Heimdalsvatn was very small in the first month after the tagging, bias caused by unusual movements shortly after tagging is of small consequence.

V. AGE AND GROWTH

A. Back-calculation of growth from scales

DAHL (1910) showed that the age of brown trout could be read from the scales. This has been confirmed by many later authors, and all over the world the scales are commonly used for ageing trout.

In the same paper DAHL showed that back-calculation of growth from trout scales gave results with sufficient accuracy for practical use, when he assumed that the scale radius grew in proportion with the total length of the fish. The same method, later called LEA—DAHL's method had then for some time been tried by LEA on herring and sprats.

DAHL was already in 1910 aware that fish and scale did not grow exactly in proportion during the whole life of the fish. The exact relation between scale growth and fish growth has later been treated in a voluminous literature. A survey of the early articles about the subject was given by GRAHAM (1929).

LEA's simple formula $l = as$ which describes the relation between fish length l and scale radius s as proportional had to be modified for certain fish species, and different equations of varying merit and complication have been used. The simplest modification was the still linear $l = a + bs$ where a and b are constants. Later followed second or third degree polynomials and logarithmic transformations — the history was recently reviewed by HILE (1970). Nearly all these models were built on the assumption that the body-scale relationship can be described with sufficient accuracy by some simple formula. This implies trying curves based on the *a priori* formula on plots of scale dimension — fish dimension. A close fit of the curve through the whole range of the observed dimensions can then be taken as a proof that the mathematic model describes the observed material, but extrapolation outside the observed range may give errors. A more direct approach was tried by SEGERSTRÅLE (1933) who emphasized the advantage of using an empirically derived length-scale curve and developed a simple graphic method to use this curve for back-calculations. This procedure eliminates errors due to the choise of a wrong formula to describe the growth, but as fitting of the curve by eye is necessary, numerous sets of length-scale measurements are required. Also by this method extrapolations are dangerous.

Whether the curve describing the body-scale relation is made from the fit of a formula to the observations or by SEGERSTRÅLE's empiric method, it is always based on averages of observations. Usually the scatter of the points representing paired values of scale radii and fish lengths is considerable. The question arises whether a fish with scales smaller or bigger than the mean, during its whole life has followed the average curve for scale growth. SCHINDOWSKI and TESCH (1956) assumed that for any constant fish length the scale radius values were normally distributed. A necessary condition for correct back-calculation by SEGERSTRÅLE's method was then that the scale radius and its standard deviation were proportional.

For brown trout back-calculation has usually been made without correction, as if scale and fish were growing according to LEA's simple formula. However, any formula can at best give an approximate quantitative description of results of the complicated processes involved in the increase of fish lengths and scale lengths with time. As shown by KIPLING (1962) there can be considerable

Table 5. *Linear regression of log l on log $\bar{s}$.*

Year	No. of fish	Range in length (cm)	b_{yx}	0.95 conf. interval of b_{yx}
1958	57	16.5—37	0.86	0.73—0.98
1965	101	16.5—51	0.97	0.91—1.04
1966	100	16.5—51	1.03	0.96—1.11
1969	89	10 —41	0.96	0.89—1.03

difference in the relationship scale length—fish length between different stocks of trout, and the relationship appeared in her material to be correlated with the growth rate. Where accurate back-calculation of trout growth is wanted, an examination of this relationship is therefore needed for the trout population studied.

In our material scale impressions on celluloid were used for analysing the fish length—scale length relationship.

For each of the years 1958, 1965, 1966 and 1969 four fish were randomly picked from each available centimetre group. The number of fish examined is shown in Table 5. Three randomly picked scale impressions from each of these fish were measured. On the projected image of the scale the distance, s, from the centre to the anterior edge was measured in arbitrary units. An anova showed the "between fish of the same length" variation to be significantly greater than the "between scales within the same fish" variation. This is in accordance with KIPLING's results. The arithmetic mean, $\bar{s}$, of the three scales from a fish was plotted against the corresponding fish length. The plot showed an increased scatter of the points as the fish lengths increased.

Fisrt and second degree regressions of l on $\bar{s}$ were computed. Analysis of the regressions gave no indications of curvature. Hence, straight regression lines were fitted to the data for the four years by the least squares method. The extrapolated lines cut the l-axis on both sides of the origin and near this point.

Logarithmic transformation, as used by KIPLING, was tried and the regression coefficient b_{yx} for log l on log $\bar{s}$ calculated for the four years. The results are shown in Table 5.

The regression coefficient, b_{yx}, is close to 1.0 in the years 1965—69, hence the growth of fish and scale isometric for fish within the tabulated ranges. The smaller value for b_{yx} in 1958 when the growth was slower, may indicate that KIPLING (1962) was right in assuming a connection between slow growth in length and allometry in length growth—scale growth.

Direct proportion between scale growth and length growth was accepted for trout down to 15 cm. The available number of fish shorter than 15 cm was too small to justify any assumption about their scale growth.

B. *Bias in back-calculated growth due to gear selectivity*

Reasonably accurate back-calculation of the growth can now be made for the individual fish. But when the individual growth data shall be combined to calculate the growth rate of a trout stock new difficulties arise because of size-selective mortality and size-selective sampling. SUND (1911), who examined sprat samples, found that: "The

Table 6. *Mean back-calculated lengths 1958.*

Age	N	l_1	l_2	l_3	l_4	l_5	l_6	l_7	l_8	l_9	l_{10}	l_{11}	l_{12}
3	2	4.0	9.0	13.0	—	—	—	—	—	—	—	—	—
4	15	3.4	7.5	11.4	15.7	—	—	—	—	—	—	—	—
5	5	3.0	6.4	11.2	14.2	18.4	—	—	—	—	—	—	—
6	18	3.4	7.6	12.6	16.6	20.1	23.3	—	—	—	—	—	—
7	50	3.5	7.9	12.3	16.0	19.4	22.2	24.6	—	—	—	—	—
8	70	3.4	7.5	11.7	15.2	18.1	20.8	23.1	25.1	—	—	—	—
9	48	3.3	6.8	11.2	14.6	17.5	20.2	22.6	24.5	26.2	—	—	—
10	11	3.0	6.2	10.1	13.4	15.6	17.9	20.2	22.5	23.8	25.5	—	—
11	2	3.0	6.5	10.5	14.5	17.5	19.5	21.5	23.0	25.5	27.0	28.0	—
12	1	—	6.0	11.0	16.0	19.0	22.0	24.0	26.0	27.0	28.0	30.0	31.0

Table 7. *Mean back-calculated lengths for different age groups.*

Year	4 years		5 years			6 years				7 years					8 years					
	N	l_4	N	l_4	l_5	N	l_4	l_5	l_6	N	l_4	l_5	l_6	l_7	N	l_4	l_5	l_6	l_7	l_8
1958	15	15.7	5	14.2	18.4	18	16.6	20.1	23.3	50	16.0	19.4	22.2	24.6	70	15.2	18.1	20.8	23.1	25.1
1959	16	17.3	49	16.7	20.3	87	16.3	19.9	22.8	120	16.4	19.9	22.9	25.5	132	15.2	18.7	21.8	24.3	26.5
1960	34	17.1	116	16.1	20.1	191	15.9	19.4	23.0	166	15.6	19.0	21.9	24.9	109	15.0	18.2	21.4	24.2	26.6
1961	86	17.5	82	15.7	20.2	175	15.1	18.6	22.6	165	15.6	18.7	22.2	25.6	99	15.1	18.6	21.3	24.2	26.9
1962	40	18.8	200	16.3	21.3	116	15.0	19.1	23.3	130	14.8	18.2	22.3	25.8	77	15.1	18.1	21.4	24.7	27.4
1963	174	17.4	104	16.7	20.2	158	15.0	19.4	22.7	54	14.6	18.9	23.4	26.3	40	15.2	18.6	22.1	25.7	28.2
1964	140	18.0	244	15.6	21.1	108	15.0	18.7	24.1	66	14.9	19.2	22.6	27.5	17	13.8	17.8	22.1	25.6	30.1
1965	63	17.7	252	16.1	22.1	192	15.6	20.5	26.1	52	15.9	20.0	24.2	29.0	31	15.3	19.3	22.9	27.1	31.4
1966	66	17.4	204	16.5	21.2	291	15.2	20.6	25.0	94	15.0	19.6	24.7	28.4	13	17.1	21.8	26.6	30.3	33.5
1967	29	16.4	120	15.6	20.6	201	15.5	19.7	25.0	173	14.2	18.7	22.7	27.0	55	13.2	17.6	22.2	25.7	29.2
1968	62	16.8	142	15.7	19.9	170	14.9	19.4	23.3	204	14.7	18.6	23.2	26.6	99	13.4	17.7	21.4	25.8	28.6
1969	109	17.1	206	15.9	21.7	268	15.1	18.8	24.5	149	15.0	19.0	22.9	27.5	94	14.8	18.3	22.7	25.9	29.7
1970	105	19,5	301	16.1	22.8	197	15.2	20.2	26.0	169	15.2	18.7	24.5	29.9	106	14.7	18.6	22.4	27.3	31.8
1971	413	18.1	184	16.9	23.4	268	15.6	21.9	27.9	145	15.3	20.7	27.0	31.9	104	14.6	18.5	23.8	29.4	33.4

Year	9 years							10 years								11 years								
	N	l_4	l_5	l_6	l_7	l_8	l_9	N	l_4	l_5	l_6	l_7	l_8	l_9	l_{10}	N	l_4	l_5	l_6	l_7	l_8	l_9	l_{10}	l_{11}
1958	48	14.6	17.5	20.2	22.6	24.5	26.2	11	13.4	15.6	17.9	20.2	22.5	23.8	25.5	2	14.5	17.5	19.5	21.5	23.0	25.5	27.0	28.0
1959	68	14.5	17.5	20.4	22.9	25.1	27.0	30	14.0	16.7	19.3	21.7	23.7	25.6	27.4	10	14.8	17.6	20.4	22.9	24.8	26.6	28.4	29.8
1960	70	14.6	17.9	20.8	23.4	25.7	27.9	37	14.6	17.3	20.1	22.6	24.9	26.9	28.6	13	14.0	16.7	19.5	22.0	24.3	26.5	28.4	30.2
1961	49	15.0	18.1	21.0	23.5	25.9	28.2	30	14.9	18.0	21.0	23.4	25.4	27.3	29.2	14	14.9	17.8	20.1	22.5	24.5	26.4	28.2	30.0
1962	32	14.7	18.1	21.0	24.0	26.6	28.9	21	14.7	18.0	21.4	24.1	26.4	28.7	30.5	11	13.8	17.3	20.1	23.3	25.4	27.3	29.4	31.5
1963	21	15.1	18.5	22.0	25.3	28.0	30.1	15	15.5	19.2	22.2	25.2	28.2	30.9	33.2	4	15.1	18.0	20.4	22.9	25.5	27.7	29.7	31.3
1964	16	13.6	16.9	20.3	24.4	27.3	30.6	5	14.0	17.0	19.6	22.8	25.0	27.0	29.4	1	12.0	15.0	20.0	25.0	27.0	30.0	32.0	34.0
1965	5	14.4	18.6	22.6	25.8	29.2	32.4	1	18.0	22.0	25.0	28.0	30.0	33.0	36.0	2	20.0	23.5	26.5	31.0	34.0	36.5	39.0	42.5
1966	6	15.6	19.2	23.2	27.3	30.3	33.0	6	17.4	22.6	26.7	31.4	34.8	37.5	39.8	0	—	—	—	—	—	—	—	—
1967	12	12.3	15.8	20.0	24.5	27.5	29.7	3	14.7	17.6	20.9	24.6	27.9	30.0	31.2	2	16.7	19.4	23.1	27.0	30.6	32.3	35.4	37.4
1968	18	13.3	17.2	21.1	24.6	27.7	30.0	2	15.4	19.4	23.2	27.9	30.7	33.5	35.6	1	17.8	21.8	25.8	31.6	34.0	39.1	43.6	47.3
1969	23	13.7	17.3	21.4	25.4	28.6	32.0	2	13.1	16.8	21.1	25.0	29.0	31.2	34.1	0	—	—	—	—	—	—	—	—
1970	31	14.4	18.3	23.0	26.7	30.7	34.3	6	13.6	17.7	21.6	26.5	30.6	34.4	37.1	2	17.3	21.5	25.3	28.8	31.9	36.0	37.3	38.5
1971	31	15.0	19.0	23.3	27.8	31.7	34.8	5	14.9	19.1	23.7	27.7	31.8	35.7	37.9	1	15.8	19.6	23.0	25.8	28.1	30.5	33.3	34.5

Table 8. *Difference in back-calculated final length between trout from all nets and from pilot nets alone.*

Year	Age	All nets		Pilot nets		Difference
		l_n	N	l_n	N	
1959	5	20.3	49	20.5	22	−0.2
,,	6	22.8	87	23.1	32	−0.3
,,	7	25.5	120	25.7	48	−0.2
,,	8	26.5	132	26.9	52	−0.4
,,	9	27.0	68	27.2	30	−0.2
,,	10	27.4	30	28.2	14	−0.8
1960	4	17.1	34	17.0	17	0.1
,,	5	20.1	116	19.4	62	0.7
,,	6	23.0	191	23.1	83	−0.1
,,	7	24.9	166	24.7	53	0.2
,,	8	26.6	109	26.3	28	0.3
,,	9	27.9	70	27.7	27	0.2
,,	10	28.6	37	28.6	19	0
1961	4	17.5	86	17.1	37	0.4
,,	5	20.2	82	19.5	32	0.7
,,	6	22.6	175	22.9	58	−0.3
,,	7	25.6	165	25.3	41	0.3
,,	8	26.9	99	26.7	33	0.2
,,	9	28.2	49	28.1	16	0.1
1962	4	18.8	40	18.7	21	0.1
,,	5	21.3	200	20.8	99	0.5
,,	6	23.3	116	23.0	36	0.3
,,	7	25.8	130	25.9	31	−0.1
,,	8	27.4	77	27.3	23	0.1
,,	9	28.9	32	28.4	10	0.5
1963	4	17.4	174	17.1	93	0.3
,,	5	20.2	104	19.8	47	0.4
,,	6	22.7	158	22.6	65	0.1
,,	7	26.3	54	26.4	13	−0.1
,,	8	28.2	40	28.2	16	0
1964	4	18.0	140	18.0	72	0
,,,	5	21.1	244	20.9	91	0.2
,,	6	24.1	108	23.7	35	0.4
,,	7	27.5	66	28.1	27	−0.6
1965	4	17.7	63	18.3	32	−0.6
,,	5	22.1	252	21.3	102	0.8
,,	6	26.1	192	24.6	43	1.5
,,	7	29.0	52	28.7	10	0.3
1966	4	17.4	66	17.2	43	0.2
,,	5	21.2	204	20.6	89	0.6
,,	6	25,0	291	24.4	89	0.6
,,	7	28.4	94	28.3	17	0.1
1967	4	16.4	29	16.7	19	−0.3
,,	5	20.6	120	19.8	67	0.8
,,	6	25.0	201	24.3	72	0.7
,,	7	27.0	173	26.3	49	0.7
,,	8	29.2	55	28.8	13	0.4
1968	4	16.8	62	17.0	33	−0.2
,,	5	19.9	142	19.0	43	0.9
,,	6	23.3	170	21.9	30	1.4
,,	7	26.6	204	25.6	31	1.0
,,	8	28.6	99	29.6	15	−1.0
1969	4	17.1	109	17.1	34	0
,,	5	21.7	206	21.1	39	0.6
,,	6	24.5	268	23.8	46	0.7
,,	7	27.5	149	27.3	18	0.2
,,	8	29.7	94	28.5	14	1.2
1970	4	19.5	105	19.0	45	0.5
,,	5	22.8	301	22.0	70	0.8
,,	6	26.0	197	24.4	31	1.6
,,	7	29.9	169	30.8	18	−0.9
,,	8	31.8	106	32.6	9	−0.8

originally small individuals will generally attain a higher age than those which grow fast in early life" (p. 408). Lee (1912) observed that in many fish species, and among these brown trout, the back-calculated lengths from older fish were consistently smaller than those calculated from younger fish. This "phenomenon of apparent change in growth rate" is commonly called "Lee's phenomenon". A vast literature about the subject has been published. It was early shown that provided the back-calculation of growth is correct, the phenomenon can be caused by non-random sampling of the stock, by size-selective fishing mortality and by size-selective natural mortality. In the common situation where the fraction of the stock which survives after years of heavy size-selective fishing mortality, is sampled with selective gear, calculations of growth, production and yield may be strongly biased. Ways to correct these types of error were recently examined by Ricker (1969).

Table 6 shows the mean back-calculated growth for each age group in all samples from 1958. Lee's phenomenon is clearly seen — the old fish in the material have usually grown slower than the younger. Also in the samples from the later years the phenomenon is very pronounced, but in these years the gradual increase in growth due to the reduction of population densities will also tend to give the young fish a better growth than the elder fish had at the same age.

Table 7 shows the mean back-calculated growth in different years for each of the age groups 4—11 years. Back-calculated lengths smaller than about 15 cm may be biased due to allometry and the figures for l_1—l_3 have therefore been omitted. The back-calculated growth has been increasing, and this is most clearly seen from the final lengths of the elder fish. However, this growth picture can have been distorted both by size-selective fishing mortality and by selective sampling.

As shown by RICKER (1969) the non-randomness of sampling caused by selective fishing gear can bias growth calculations substantially. This may cause grave concern as most of our trout material was collected by means of gill nets.

Table 4 shows approximate values for the selectivity of the pilot nets and of the total fleets of net (including the pilot nets) used. The selectivity curves of these fleets were rather steep, and especially for fish smaller than the most vulnerable length the fleet's efficiency is quickly reduced. The pilot nets were fishing best on trout with lengths 29—35 cm, and their combined selectivity curve is much flatter. Although our general selectivity curve is inaccurate, there is no doubt that there were substantial differences in the selectivity of these groups of nets. If non-randomness due to gill-net selectivity causes substantial error in the back-calculated growth, we should therefore expect substantial differences between growth calculations based on samples from the pilot nets and on samples from the whole fleet of nets.

Table 8 shows the differences in mean back-calculated final lengths between samples from all nets and samples from the pilot nets alone. 62 growth comparisons are listed in the table. Of these 39 show a difference of 5 mm or less and 23 show differences from 6 to 16 mm. In 1959 the pilot nets gave consistently higher growth figures. In the other years the fish from the pilot nets have usually had a slightly slower growth than the fish from all nets, but there are many exceptions. The figures indicate that the errors in back-calculated length caused by selective sampling are of small consequence.

Errors in estimates of the stock's growth because of size selective fishing mortality can hardly be avoided in any trout population which has been exploited for some years with size-selective gear. However, the resulting bias in yield calculations can be reduced by calculating the instantaneous rate of increase in weight in the stock by the method mentioned by RICKER (1969). We shall return to this in the chapter about growth in weight.

C. *The length—weight relationship*

The connection between dimensions of length and weight in fishes has been examined by a very great number of authors. A review of the principal methods used and their merit was given by LE CREN (1951).

Usually the length—weight relation in fishes can be described by the general formula

$$w = al^b \tag{2}$$

where a and b are constants. If b is exactly 3.0 the fish grows isometrically, if not the growth is allometric.

A logarithmic transformation changes the equation to:

$$\log w = \log a + b \log l, \tag{3}$$

which is linear in log w and log l, and where b shows the slope of the line and log a its position.

In Norway the "condition" of individual trout or groups of trout has usually been described by a "condition factor". CF, calculated from the equation

$$CF = \frac{100\ w}{l^3} \tag{4}$$

where l is measured in centimeters and w in gram. CF can be useful for comparisons of trout of approximately the same lengths. However, if b is different from 3.0 (allometric growth) CF will vary with the fish length. This is easily seen from the expression:

$$CF = \frac{100 \cdot a \cdot l^b}{l^3} = 100 \cdot a \cdot l^{(b-3)} \tag{5}$$

If b is smaller than 3.0, CF will decrease as the fish length increases, and CF will increase with fish length if b is bigger than 3.0.

Numerous cases of length/weight allometry in brown trout have been described. Some of these are listed by CARLANDER (1969, p. 214). There is evidently considerable variation in b between various populations of trout and, as we shall see,

Table 9. *Variation in CF with length in 1965.*

Length (cm)	14.5—19.5	20—24	25—29	30—34	35—39	40—46
No.	18	104	330	120	25	7
Mean of CF	0.94	0.99	1.03	1.07	1.13	1.11

Source of variation	d.f.	Sum of squares	Mean square	F
Among length groups	5	7942	1588.40	29.32
Within length groups	598	32402	54.18	—
Total	603	40344	—	—

also variation from year to year within a discrete population.

As a first test the CF-values were computed for the 604 pairs of length—weight observations from 1965 and arranged in one-cm groups. An anova showed a highly significant variation in CF among length groups, but no significant difference in CF between juveniles of the two sexes within the same length groups. Only small differences in CF were found between juvenile and mature fish of the same length groups and sexes. Even between the mature fish of the two sexes the CF-values did not differ much, but the material was small.

The 604 CF-values were then arranged in five-cm length groups and their means were computed. The results are shown in Table 9, which also gives the results of an anova of CF for the six length groups. Again the increase in CF with length is highly significant. The most probable reason is that b is bigger than 3.0.

Fig. 6 is a plot of log weight against log length of the trout from the August 1969 samples. In order to increase the observations of small fish, the data for trout smaller than 20 cm from the September 1969 samples have been added. A sampling period of only one month was preferred to reduce eventual seasonal variations in the length—weight relation. Another kind of error may be caused by the gill-net selection, but as shown by Kipling (1957) on char and perch, satisfactory estimates of the population's regression coefficient for log w on log l can be obtained when two or more mesh sizes are used and a relatively wide range of length is covered by the sample.

As seen from the figure, a straight-line equation apparently gives a reasonably accurate description

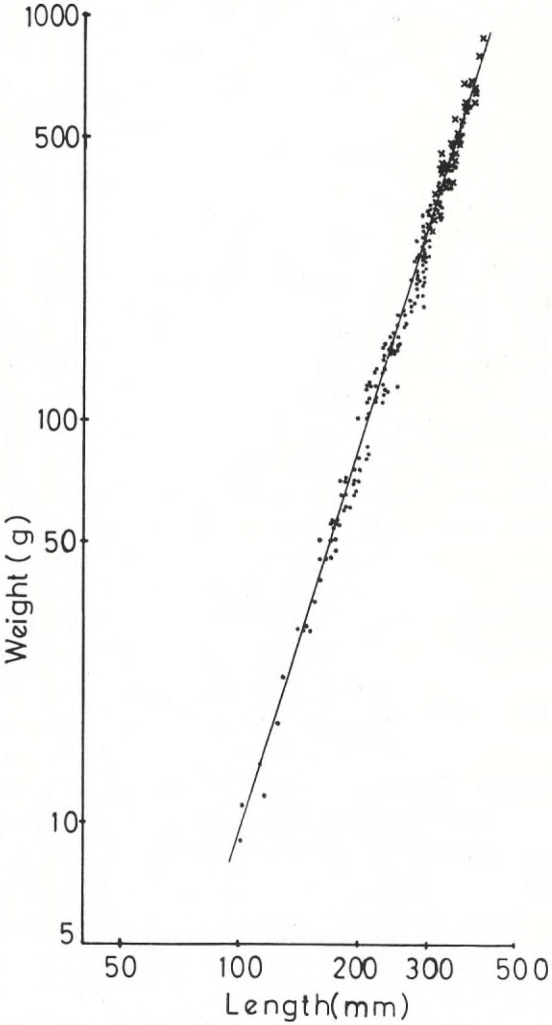

Fig. 6. Log weight—log length August—September 1969. (×=adults.)

Table 10. *Predictive and GM regressions of log w on log l.*

Year	N	r	log a	b	95 % int. for b.	v	95 % int. for v.	$\hat{w}_{200p}$	$\hat{w}_{200GM}$	$\hat{w}_{250p}$	$\hat{w}_{300p}$	$\hat{w}_{350p}$	$\hat{w}_{400p}$	$\hat{w}_{400GM}$
1957	178	0.96	–4.78	2.900	2.77—3.03	3.02	2.90—3.14	78	—	149	252	394	581	—
1958	117	0.95	–4.71	2.870	2.69—3.05	3.02	2.85—3.19	78	75	148	249	387	568	606
1959	231	0.98	–5.06	3.017	2.93—3.10	3.08	3.00—3.16	77	76	151	262	418	625	642
1960	268	0.98	–5.14	3.053	2.97—3.14	3.12	3.05—3.19	78	76	153	267	428	644	663
1961	393	0.98	–5.38	3.153	3.10—3.21	3.22	3.16—3.28	75	74	152	270	439	669	688
1962	306	0.98	–5.25	3.098	3.02—3.17	3.16	3.09—3.23	76	75	151	266	428	648	666
1963	301	0.99	–5.32	3.139	3.09—3.19	3.17	3.12—3.22	81	80	162	287	466	709	719
1964	319	0.99	–5.37	3.164	3.11—3.22	3.20	3.15—3.25	81	80	165	293	477	728	740
1965	311	0.99	–5.52	3.219	3.17—3.26	3.25	3.20—3.30	78	77	159	286	470	722	732
1966	331	0.99	–5.36	3.151	3.10—3.20	3.18	3.13—3.23	77	77	157	279	435	690	698
1967	85	0.99	–5.57	3.239	3.13—3.35	3.27	3.17—3.27	76	75	157	283	467	720	728
1968	271	0.99	–5.39	3.173	3.13—3.22	3.21	3.16—3.26	81	80	165	294	479	731	741
1969	806	0.99	–5.26	3.122	3.08—3.16	3.15	3.12—3.18	84	83	168	297	480	729	736
1970	297	0.99	–5.26	3.106	3.06—3.15	3.14	3.09—3.19	78	77	156	275	443	671	678
1971	—	—	—	—	—	—	—							
1972	—	—	—	—	—	—	—							

of the observations both for juveniles and adults. The straight line giving the best fit was computed by the regression method of least squares. Log a, the regression coefficient b, the correlation coefficient r and "Student's" t for the regression coefficient were computed. The same computations were done for the August material for each of the years 1957—70. The results are listed in Table 10 which also gives the 95 % confidence intervals for b. The regression coefficient b is independent of the units used for measuring length and weight, but log a is not. The tabulated values were computed for l listed in mm and w in gram. In each line in the table log a for fish measured in cm and gram can be found by adding b to the tabulated log a.

As seen from the table, the correlation coefficient is in all years very high. There is a general increase in b until around 1965, and in the last years a decrease. In the years 1957—60 b is not significantly different from 3.0. In all the years 1961—70 the difference is significant.

Hile (1936) mentions that there is usually a negative correlation between a and b. In our material the correlation between log a and b is very pronounced, with r=—0.998. This correlation is inevitable because in the linear regression the equation for log a is:

$$\log a = \overline{Y} - b \cdot \overline{X}$$

where $\overline{Y}$ is the mean of the logarithms of the individual weights and $\overline{X}$ the mean of the logarithms of the corresponding lengths. As there is but little variation in $\overline{Y}$ and $\overline{X}$ between years, log a is bound by the regression model to be negatively correlated with b.

Ricker (1973) showed that in bivariate distributions when both variates are subject to errors of measurement and/or inherent variability, b-values computed by this ordinary predictive regression method are consistently too small. Better estimates are obtained by computing the geometric mean estimate of the functional regression of log w on log l (the "GM regression").

This method was tried by computing the slope of the line as:

$$v = \frac{b}{r} \text{(formula 17 in Ricker 1973)}$$

and the confidence limits for v from:

$$v \pm t\left(\frac{v^2(1-r^2)}{N-2}\right)^{1/2} \qquad (6)$$

where t is "Student's"t with N—2 d. f.

The v-values and their 95 % confidence intervals are listed in Table 10.* As expected the v's are consistently higher than the b's, but as r in most years is so close to 1.0, the difference is small.

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* Better, asymmetrical, limits could probably have been obtained by using equation (1) in Ricker (1975).

As $\bar{Y}$ and $\overline{X}$ were known from the predictive regression, the new values for the Y-axis intercept could be computed.

The last seven columns in the table show estimated average weights for trout with lengths 200, 250, 300, 350 and 400 mm. For the length groups 200 and 400 mm both the GM estimates and the predictive regression estimates are listed. For the three other length groups only the predictive regression estimates are given. For 200 mm long trout the GM estimates of weight are mainly 1—2 % lower than the estimates based on the predictive regression. For 400 mm trout the GM estimates are consistently higher than the others — in 1958 by 6.7 %, in 1959—62 by 2.7—2.9 % and in 1963—70 by 1.0—1.6 %. For trout in the most common range in the catches (about 26—32 cm) the differences will be very small. In this material the eventual bias caused by choosing the predictive regression to estimate the weights of trout of known lengths will therefore be unimportant. In other trout samples with a wide range in length and r considerably smaller than 1.0 the difference between the two kinds of estimates can probably be substantial.

As seen from the table there has been a pronounced increase in weights for fish of the same lengths from 1958 to 1964 for trout from 250 mm and upwards. The moderate set-back in 1962 is probably due to the cold summer in that year. We shall later see that there was also a set-back in growth rate in 1962.

D. Growth in weight

For calculations of yield according to RICKER's method with exponential growth we need estimates of the instantaneous coefficient of growth in weight, G. As previously shown, errors due to size-selective sampling are probably unimportant for our estimates of growth in length. A comparison of G-values calculated from all the nets used and from the pilot nets alone gave also small and inconsistent differences.

However, the occurrence of LEE's phenomenon in the material indicated that size-selective mortality can be expected to influence the growth picture. For yield calculations RICKER (1969) recommends to compute G from the formula

$$G = b(\log_e L_2 — \log_e L_{1C}) \qquad (7)$$

where L_2 is the mean length at the last annulus of an age group and L_{1C} the mean length at the second last annulus of the same group. As L_2 and L_{1C} are means, b should be computed as "year-class b" (RICKER 1958).

The G-values were computed by this method and are listed in Table 11. In all years there is, as usual in fish, a consistent decline in G with age. All G-values except G_9 increase from 1958—59 to 1963—64 but with a set-back in 1962—63.

By this method the growth in the last completed growth season is computed for each year for the fish that were actually caught in that year. If the sampling is random the method should give correct G-values for the population.

As shown by RICKER (1969) errors in G caused by sizeselective mortality can be serious. In order to obtain an impression of the magnitude of this kind of error for trout, the apparent year-class growth was computed from our material. An example will explain the method used: In 1958 we have scales of 15 trout of age 4+ (year-class 1954). Survivors from this year-class were caught as five-year olds in 1959, as six-year olds in 1960 and so on, and their individual lengths when their fourth annulus was laid down in 1958 can be back-calculated and transformed to individual weights. From these again can be calculated the mean weight when the annulus was laid down for all the 524 individuals of the year-class which were sampled at age 4+ or more. In the same way we can estimate the mean weight for all trout that completed their fifth annulus in spring 1959 and were sampled in 1959 or later. G can then be computed as:

$$G_{4(-58-59)} = \log_e \overline{w}_{5(-59)} — \log_e \overline{w}_{4(-58)} \qquad (8)$$

This method was used. The transformation of individual length to weight was done from

$$w = a \cdot l^b$$

where a and b for each growth year were the predictive regression values listed in Table 10. The resulting, biased, G-values were, as expected, consistently lower than the values estimated by RICKER's method. In most cases the biased values were 10—25 per cent too low.

E. Growth rate and maturity

DAHL (1917) found that the trout in Eastern Norway and in the mountain lakes usually grew faster, became bigger and attained maturity at a higher age than in Western Norway, where the lakes were often teeming with small, slow-growing trout which spawned at a young age. He demonstrated the pronounced density dependence of trout growth, but did not draw the conclusion that a decrease in trout growth due to overcrowding caused a lower age at first maturity.

HUITFELDT-KAAS (1927, p. 245) states: "All river-trout seem to be particularly early spawners and when young spawn intensely. The same appears to be the case with practically all slow-growing and small-grown trout-tribes from the lakes. On the other hand practically all large-grown and quick-growing tribes seem to have a somewhat late and tardily occurring spawning. From these many single observations pointing in the same direction I draw the conclusion *that starvation (lack of food) tends to hasten the propagation of the fish and increases its intensity.* From a teleological point of view such a theory should be apparently wellgrounded." — — — "In my opinion the reproduction in fish hastened by lack of food must be regarded in quick essential degree as tending to set back the already previously famished tribes of fish, in growth and in normal size, and tends to produce a speedy modification in the direction of dwarf-formation."

After HUITFELDT-KAAS' paper the connection between growth rate and maturity in brown trout was commented on by many authors, but as possible genetic differences were not taken in account, the results were confusing. Reviews of the literature about the subject were given by ALM (1959) and NIKOLSKII (1969).

ALM studied very carefully and painstakingly in a series of pond experiments the causal relationship between growth, size, age and maturity in different tribes of brown trout and several other freshwater species. From his conclusions can be cited (ALM, 1959 p. 115): *"In a population with good growth rate maturity appears at a lower age and usually also at a smaller size than in a population with poor growth rate, where maturity is reached only at a higher age and in most cases at a bigger size. In populations with very poor growth rate and high age for maturity the average length at maturity can again be lower, and approach that of the earliest mature and most fast-growing populations."* — — — *"Whenever experiments that could really be checked have been carried out, it has been established with regard to the same form or species that early maturity is connected with good growth, and later maturity with poor growth."*

For the management of trout lakes an association between growth rate and age at first maturity could be important. In overcrowded trout lakes reduction of the population density will usually result in faster growth and higher yields, but a part of this increase could be written off as an increased surplus production of eggs and milt. We shall show that this did not happen in our experimental lake.

In the material the gonad development was, as usual in Norway, described by the system introduced for trout by DAHL (1917). In female trout the residual eggs can often be used to differentiate first-time spawners from fish which have spawned in a previous season. They can also be used to distinguish between juvenile females and females which "take a rest" after having spawned in a previous year. Further, female trout which have spawned, have much longer ovaries than juvenile specimens. Already in July the ovaries of many trout have reached the maturing stages III or IV, and these fish will spawn in the coming autumn. Females in stage II in the first half of July may stay juvenile, but as there is considerable individual variation, some of them may later in July develop to stage III and spawn in the coming autumn. In our lake an unbiassed separation of the juvenile female trout from the adults can therefore best be done towards the end of July or in August.

For male trout it is often very difficult or even impossible by eye to separate juvenile fish in stage II from previous spawners in stage VII/II. It may likewise be impossible without the microscope to separate first-time adults (stages III, IV, V, VI) from maturing previous spawners (stages VII/III, VII/IV, VII/V, VII/VI). As shown (JENSEN 1953) this can be done by microscopic examination of sections of the testes, but the method is too time-consuming for practical use. Sometimes secondary

Table 11. *G-values for different years.*

Year	G_4	G_5	G_6	G_7	G_8	G_9	G_{10}	G_{11}
1958—59	0.66	0.46	0.37	0.29	0.25	0.23	0.16	—
1959—60	0.69	0.53	0.40	0.29	0.26	0.19	0.19	—
1960—61	0.80	0.61	0.45	0.34	0.28	0.21	0.20	—
1961—62	0.90	0.68	0.50	0.35	0.28	0.21	0.23	0.18
1962—63	0.63	0.52	0.39	0.32	0.24	0.24	—	—
1963—64	1.00	0.84	0.65	0.53	0.38	0.28	—	—
1964—65	0.97	0.73	0.55	0.45	0.32	—	—	—
1965—66	0.80	0.62	0.45	0.32	0.27	0.19	—	—
1966—67	0.90	0.77	0.56	0.41	0.25	—	—	—
1967—68	0.75	0.58	0.44	0.33	0.25	—	—	—
1968—69	1.03	0.88	0.61	0.46	0.34	—	—	—
1969—70	1.00	0.73	0.58	0.44	0.32	—	—	—
1970—71	1.02	0.76	0.53	0.40	0.29	—	—	—

sexual characters (long upper jaw, hook on lower jaw, thickened skin) will decide the issue, but especially in small trout these characters may be absent also in the spent fish. The scales are usually loosely embedded in the skin of juvenile trout while they in adults may be difficult to scrape off because of the thickened skin. But there are exceptions from this rule — I have examined previous spawners with loose scales, but never juvenile trout with the scales very firmly attached. As only macroscopic examination could be done, some "resting" male trout in the material may have been classified as juveniles.

Of greater concern is bias due to the spawning migration. The males do probably begin their spawning migration earlier and stay in the river or beck for a much longer time than the females (Sømme, 1941). This will cause an under-representation especially of the adult males in samples taken in the lake shortly before or during the spawning period. In Ø. Heimdalsvatn the spawning places are found in the outlet river and to a smaller extent in the biggest of the inlet becks. The spawning takes mainly place in the second half of September and the first half of October, but some ripe males enter the outlet river already in the second half of August. These fish are then outside the reach of the nets in the lake during a part of the best fishing time. On the other hand an increased acitivity by the adults before and during the spawning migration (Sømme, 1941) may tend to give an over-representation of spawners in the gill-net catches.

Because of these sources of error August samples will probably give the best estimates of the fraction of adult fish in the different age groups. However, as the September—October samples of females showed no great difference from the August samples, all samples of females from August to October were pooled. The results are shown in Table 12. In the males the fraction of spawners was considerably lower in the samples from September—October than in August, and therefore only the August samples are included in Table 13. The tables show for each age the total number of fish in the samples and the per cent adults.

With the exception of a single maturing (stage V) three years old male caught in August 1968, four years is the lowest age at maturity in both sexes, and only a few fish attain maturity at this age. As seen from the tables even in 1958, when the growth was slow, a considerable number of females of high age had not attained maturity. The males give the same impression, but here some of the "resting" specimens may have been labelled as juveniles.

Most striking is the decrease in the number of adults between 1958—59 and 1965. In 1959 53 per cent of the females in the sample were adults — in 1965 the percentage of adults had decreased to nine. In the August material from 1958 70 per cent of the males were adults — in 1965 only seven per cent.

The increased fishing mortality has of course reduced the number of old fish in the samples, but

Table 12. *Total numbers and percent adults of female trout in August—October samples.*

Year		Age												Total
		2	3	4	5	6	7	8	9	10	11	12	13	
1958	N	—	—	7	1	7	23	28	24	3	—	—	—	93
,,	% ad.	—	—	0	0	43	52	32	25	33	—	—	—	31
1959	N	—	2	3	17	34	64	51	28	5	4	—	—	208
,,	% ad.	—	0	0	12	38	70	61	46	60	75	—	—	53
1960	N	—	3	13	38	88	64	44	16	7	1	—	—	274
,,	% ad.	—	0	8	3	16	34	61	81	57	100	—	—	30
1961	N	—	6	41	36	87	87	45	26	7	4	—	—	339
,,	% ad.	—	0	2	6	10	45	51	92	71	75	—	—	31
1962	N	—	16	15	95	59	69	42	11	5	2	3	—	317
,,	% ad.	—	0	0	0	2	19	31	55	60	0	100	—	12
1963	N	—	9	74	49	76	25	19	12	6	1	1	—	272
,,	% ad.	—	0	0	0	0	16	37	75	83	100	100	—	10
1964	N	—	6	57	108	62	34	8	9	2	—	1	1	288
,,	% ad.	—	0	0	0	15	26	38	78	50	—	100	0	10
1965	N	—	1	28	118	108	35	14	1	1	—	—	—	306
,,	% ad.	—	0	0	1	3	46	36	0	100	—	—	—	9
1966	N	—	3	37	93	142	48	3	3	5	—	—	—	334
,,	% ad.	—	0	0	3	6	29	100	67	100	—	—	—	11
1967	N	—	6	13	46	106	103	26	4	1	2	—	—	307
,,	% ad.	—	0	0	0	7	12	35	50	100	100	—	—	11
1968	N	—	3	27	64	83	119	59	10	—	—	—	—	365
,,	% ad.	—	0	0	3	4	24	27	40	—	—	—	—	15
1969	N	2	7	30	82	123	68	25	7	—	—	—	—	344
,,	% ad.	0	0	0	2	10	54	84	57	—	—	—	—	22
1970	N	—	17	38	80	68	64	36	4	1	—	—	—	308
,,	% ad.	—	0	0	1	4	55	81	100	100	—	—	—	24

the decrease in number of adults is only partly caused by this. The tables show that also within each of the young age groups five, six and seven years, there is a pronounced decrease in the fraction of adults. The observations made by HUITFELDT-KAAS and others are in this way confirmed: Reduction by heavy fishing of a dense trout population can result in an increased age at first maturity. As the density reduction usually causes better growth, it might easily be concluded — as HUITFELDT-KAAS and others did — that the increased growth by itself causes the delay in maturity. This is, however, strongly contradicted by ALM's careful experiments. A possible explanation is that the observed decrease in adults in the younger age groups is caused by the selectivity of the fishing gear. The finemeshed gill nets used until August 1965 had a much higher fishing power on trout smaller than 28 cm than the net fleets used from August 1965 to June 1971 (Table 4). Therefore the fastest growing fish of the younger age groups present in the lake were more efficiently sorted out and killed in 1958—65 than in 1966—71. As the fastest growing individuals in the year-class first attain maturity, this selective mortality could be expected to cause an increased age at first maturity in the surviving fraction of the year-class.

After 1965 the reduced fishing mortality among the youngest age groups gave the fastest growing youngsters a better chance to attain maturity before they were caught, and this may explain the increasing number of adults after 1965.

In June 1971 the mesh size was again changed to meshes that will cause a very high fishing mortality on young trout. This is expected to cause a new increase in age at first maturity.

VI. THE VIRTUAL POPULATIONS

The concept "virtual population" as used by FRY (1949) means simply the number of fish alive at a chosen time, which will be caught in future. In a recent article RICKER (1971) reviewed the history of the idea and examined some of the

Table 13. *Total number and percent adults of male trout inAugust samples.*

Year		Age													Total
		2	3	4	5	6	7	8	9	10	11	12	13	14	
1958	N	—	—	1	2	6	13	21	19	3	—	1	—	—	66
,,	% ad.	—	—	0	0	33	69	81	79	33	—	100	—	—	70
1959	N	2	1	5	15	22	23	31	12	12	2	—	—	—	125
,,	% ad.	0	0	0	13	9	30	42	50	33	100	—	—	—	29
1960	N	—	—	9	26	17	38	20	20	11	3	—	—	—	144
,,	% ad.	—	—	0	0	12	8	30	50	27	67	—	—	—	26
1961	N	—	5	20	20	45	47	37	16	20	8	2	—	—	220
,,	% ad.	—	0	0	0	0	2	22	56	60	50	0	—	—	15
1962	N	—	5	10	40	29	33	16	10	6	3	2	1	—	155
,,	% ad.	—	0	0	0	0	3	13	20	67	33	100	100	—	8
1963	N	1	1	41	39	49	17	12	4	5	2	—	—	—	171
,,	% ad.	0	0	0	0	0	0	42	50	40	0	—	—	—	5
1964	N	—	1	40	68	22	14	6	4	2	1	—	—	—	158
,,	% ad.	—	0	0	0	0	0	17	50	50	0	—	—	—	3
1965	N	—	1	21	71	40	11	8	1	—	2	—	—	—	155
,,	% ad.	—	0	0	0	0	36	13	0	—	100	—	—	—	7
1966	N	—	5	17	42	73	26	7	1	—	—	—	—	—	171
,,	% ad.	—	0	0	0	1	15	57	100	—	—	—	—	—	6
1967	N	—	—	2	12	17	14	5	—	—	—	—	—	—	50
,,	% ad.	—	—	0	0	0	0	0	—	—	—	—	—	—	0
1968	N	—	6	14	16	33	26	24	3	2	—	—	—	—	124
,,	% ad.	—	17	0	0	0	12	29	67	50	—	—	—	—	11
1969	N	3	6	44	66	85	40	25	5	2	—	—	—	1	277
,,	% ad.	0	0	11	32	38	45	92	80	100	—	—	—	100	38
1970	N	1	11	18	46	29	18	15	6	4	—	—	—	—	148
,,	% ad.	0	0	0	4	7	22	67	67	100	—	—	—	—	18

merits of using virtual populations to estimate vital statistics (the "biostatistical" method).

Virtual populations can only be calculated in retrospect after all fish in the year-classes involved are dead. As the fish dying from natural mortality are left out, the virtual population will be a minimum estimate of the number of fish present at a certain time, provided that no immigration after that time take place in the year-classes concerned.

For each of the years 1958—71 the monthly age distribution in the total catch was estimated from the monthly age distribution in the scale samples. These data were used to calculate the year-class distribution in the whole catch for each year. The results are shown in Table 14. From this table the virtual populations have been calculated, and these are shown in Table 15. We shall later use the virtual populations to control estimates of survival from tagging (Chapter VII) and to estimate the true populations (Chapter VIII).

VII. NATURAL MORTALITY

Little is known about the natural mortality in wild populations of brown trout living in lakes. One reason for this is that usually the natural mortality can only be estimated indirectly and this usually necessitates reliable estimates of both the rate of survival and of the fishing mortality during the same time period.

Frost and Smyly (1952) estimated a yearly survival rate of $\hat{S}=0.35$ for trout between four and eight years in a moorland pond in the Lake District. The corresponding exponential coefficient of total mortality is $\hat{Z}=1.05$. As some fishing took place, the exponential coefficient of natural mortality, M, must have been smaller than 1.05. Otters were present at least in part of the experimental period and may have caused an unusually high natural mortality.

Ball and Jones (1962) estimated the annual survival rate of one to four-year-old trout in Llyn Tegid to vary between $\hat{S}=0.24$ and $\hat{S}=0.33$

Table 14. *Estimated year-class distribution in the catch.*

Year	Year-class																								
	1946	—47	—48	—49	—50	—51	—52	—53	—54	—55	—56	—57	—58	—59	—60	—61	—62	—63	—64	—65	—66	—67	—68	—69	—70
1958	14	15	131	674	869	623	231	45	148	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1959	1	1	18	113	236	471	437	342	201	76	15	8	—	—	—	—	—	—	—	—	—	—	—	—	—
1960	—	—	1	85	138	269	505	675	715	353	135	8	—	—	—	—	—	—	—	—	—	—	—	—	—
1961	—	—	—	5	51	109	203	363	689	731	362	356	65	—	—	—	—	—	—	—	—	—	—	—	—
1962	—	—	3	6	23	17	54	91	247	442	362	529	106	91	—	—	—	—	—	—	—	—	—	—	—
1963	—	—	—	—	7	5	8	33	71	103	225	602	395	603	51	5	—	—	—	—	—	—	—	—	—
1964	—	—	—	—	1	1	1	1	13	45	59	189	417	1014	506	38	—	—	—	—	—	—	—	—	—
1965	—	—	—	—	—	1	—	—	2	5	13	94	148	573	641	156	14	—	—	—	—	—	—	—	—
1966	—	—	—	—	—	—	—	—	—	—	14	16	37	253	857	547	136	37	—	—	—	—	—	—	—
1967	—	—	—	—	—	—	—	—	—	—	4	7	26	162	565	602	305	66	43	—	—	—	—	—	—
1968	—	—	—	—	—	—	—	—	—	—	—	1	7	39	231	435	353	258	101	35	—	—	—	—	—
1969	—	—	—	—	—	—	—	—	—	1	—	—	—	2	24	105	163	311	229	118	20	8	—	—	—
1970	—	—	—	—	—	—	—	—	—	—	—	—	—	3	7	39	133	210	242	364	121	50	3	—	—
1971	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	11	45	151	210	383	280	719	367	1	—
Σ:	15	16	153	883	1325	1496	1439	1550	2086	1771	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Table 15. *Virtual populations.*

Year	Year-class																			
	1945	—46	—47	—48	—49	—50	—51	—52	—53	—54	—55	—56	—57	—58	—59	—60	—61	—62	—63	—64
1958	—	15	16	153	883	1315	1496	1439	1550	2086	1771	—	—	—	—	—	—	—	—	—
1959	—	1	1	22	209	446	873	1208	1505	1938	1756	1189	1810	—	—	—	—	—	—	—
1960	—	—	—	4	96	220	402	771	1163	1737	1680	1174	1802	—	—	—	—	—	—	—
1961	—	—	—	3	11	82	133	266	488	1022	1327	1039	1794	1201	—	—	—	—	—	—
1962	—	—	—	3	6	31	24	63	125	333	596	677	1438	1136	2739	—	—	—	—	—
1963	—	—	—	—	—	8	7	9	34	86	154	315	909	1030	2648	2885	—	—	—	—
1964	—	—	—	—	—	1	2	1	1	15	51	90	307	635	2045	2834	—	—	—	—
1965	—	—	—	—	—	—	1	—	—	2	6	31	118	218	1031	2328	—	—	—	—
1966	—	—	—	—	—	—	—	—	—	—	1	18	24	70	458	1687	—	—	—	—
1967	—	—	—	—	—	—	—	—	—	—	1	4	8	33	205	830	—	—	—	—
1968	—	—	—	—	—	—	—	—	—	—	1	—	1	7	43	265	—	—	—	—
1969	—	—	—	—	—	—	—	—	—	—	1	—	—	—	4	34	—	—	—	—
1970	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	10	—	—	—	—
1971	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—

with a mean of $\hat{S}=0.29$ which corresponds to $\hat{Z}=1.24$. The low survival rate can partly be explained by the presence of pike and perch in Llyn Tegid, but also from methodical errors. The survival rate was computed from density indices obtained by means of hauls with a 90 feet long small-meshed (1/4 inch) shore seine. As the mesh retained all trout longer than about 40 mm, the authors concluded that the mesh was not selective for size. However, as the swimming speed of trout increases with the length, the catchability of trout in a slow-moving, small-meshed seine is probably decreasing with the fish length, and this will give too low survival estimates.

In Ø. Heimdalsvatn the rate of survival can be estimated by tagging and recapture through series of years, and as all fish killed by fishing have been recorded, the average natural mortality in different years can be estimated. Data have also been obtained from two other trout lakes. However, before we analyse this material, we must examine the possibility of serious errors caused by tag losses.

A. Tag losses

When marking or tagging is done at the start of the fishing season in two consecutive years, the rate of survival in the time between the end of the marking in year 1 and the beginning of the marking in year 2 can be estimated by the formula (5.2 in RICKER, 1958):

$$\hat{S}=\frac{r_{12}\cdot m_2}{m_1(r_{22}+1)} \tag{9}$$

where r_{12} is the number of recaptures of first-year marks in the second year

r_{22} is the number of recaptures of second-year marks in the second year

m_1 is the number of fish marked in year 1

m_2 is the number of fish marked in year 2.

However carefully the operations are done, the handling and stressing of the trout by capture and marking or tagging will probably give an increase in "natural" mortality in the first few days after tagging and release. If the fraction of released fish dying shortly after the release is constant from year to year, m_1 and m_2 will be reduced by the same factor, and this will not influence $\hat{S}$.

Errors caused by tag losses can be serious. Extensive losses of tags by brown trout in Swedish mountain lakes were reported by FAGERSTRÖM *et al.* (1969), but this was probably due to the inferior tagging technique used (single nylon thread, loose attachment).

If tags are lost at a constant rate, the rate of tag retention can be estimated by the method worked out by ROBSON and REGIER (1966) and survival estimates that are unbiased from tag loss be obtained.

One of the ways to examine tag losses is to compare the recaptures of tagged fish with recaptures of fish that were marked by methods not involving the use of mechanic tags. In 1959 and 1960 every second fish was alternatively tagged or marked by fin-cutting. In 1959 the adipose was removed and in 1960 the left ventral fin. The results are shown in Table 16. From both groups in 1959 52 % were later recaptured. Of the fish tagged in 1960 54 % were later recaptured, while only 44 % were recaptured of the fin-cut specimens. The difference is not significant ($P=0.31$).

Apparently there is no great difference between the total number of recaptures of fin-cut and of tagged trout. However, the material is small, and eventual tag losses may have been masked by an increased catchability of the tagged specimens because the tags can be entangled in the nets.

Another approach was to add a second tag on all previously tagged trout that were recaptured on chase net or hook and returned alive to the water. This was done in 1966—69, and the second CARLIN tag was attached to the back of the fish closely behind the dorsal fin. My hope was that this second tag, which was attached one, two or more years after the first tag, should still keep in position after the first tag eventually was lost. Unfortunately the opposite happened: Many fish were recaptured with the first tag firmly attached while tag no. 2 had been lost.

The best evaluation of the tag loss was obtained by cutting away the adipose fin on all trout that were tagged in the years 1966—70. The adipose does not regenerate if properly removed (DAHL 1939, STUART 1958) and its removal does neg-

Table 16. *Comparison of recaptures of marked and tagged trout.*

Year of marking (tagging)	Marked by fin-cutting							Tagged						
	No. marked	Recaptures (number)						No. tagged	Recaptures (number)					
		1959	1960	1961	1962	1963	Total		1959	1960	1961	1962	1963	Total
1959	44	6	15	2	—	—	23	42	8	12	1	1	—	22
1960	48	—	11	9	—	1	21	46	—	12	9	4	—	25

ligible harm to the fish. Examination of tens of thousands of trout through the years has convinced me that lack of the adipose due to natural causes occurs very seldom indeed in Norwegian trout. From 1966 all trout captured in the lake have been carefully examined and specimens without the adipose and without tag have been registered. The results are shown in Table 17. The one specimen recaptured in 1967 with the tag missing had completely fresh scars after the tag, and probably the tag was lost when the fish was taken out of the net. Two of the three fish with missing tags in 1968 had completely fresh tag-scars, and the tags were probably lost when a careless "helper" squeezed the fish through the meshes. Anyhow, the figures in the table show that at least in the year of tagging and in the following year the lag losses are negligible.

From all recaptured trout that have been killed, the tag have been removed. To draw out by hand the tag from trout that had been tagged the same year was always difficult. Some of the tags were more easily removed the year after tagging, and two or more years after tagging the tags could often very easily be drawn out by hand. In many cases deep, cataract-like wounds were found on both sides where the wires penetrate the skin, and these wounds seemed to grow in size with time. The observations indicate that the tags are lost at an increasing rate.

B. Estimates of survival and natural mortality from tagging

Table 18 shows the number of trout tagged and the per cent recaptured in different years. Year 1 in the table is the year of tagging.

The material has been divided in fish that were 26 cm or smaller and fish bigger than 26 cm at the time of tagging. As seen the rate of recapture in year 1 is usually considerably higher for the bigger fish than for the small ones. The reason is probably that the smaller fish were not fully vulnerable to the gill nets in the year of tagging. This will tend to make r_{11}/m_1 smaller than the true rate of exploitation for the fully vulnerable fish sizes. Bias from this can be avoided by basing the survival estimates on only those tagged fish which in both years had a sufficient size to be fully vulnerable to the fishing gear. We shall there-

Table 17. *Recaptures of trout both tagged and marked.*

Year of tagging	No. tagged	No. recaptured with tag attached						
		1966	1967	1968	1969	1970	1971	Total
1966	217	74	45	10	3	4	—	136
1967	201	—	83	48	5	2	1	139
1968	179	—	—	96	24	6	5	131
1969	224	—	—	—	114	35	31	180
1970	302	—	—	—	—	86	107	193
		No. recaptured with tag lost						
		0	1	3	1	4	5	14

fore in the survival estimates exclude all trout which were 26 cm or smaller when they were tagged.

In the years 1958—60 changes were frequently made in the composition of the fleet of gill nets used, and the number of tagged fish was very small. In 1965 the method used gave negative natural mortality, which is meaningless. The reason was probably that a profound change in gill-net composition took place in the middle of the fishing season in that year (Table 2). New important changes in the gill-net composition were made in 1969—71. Because of these changes in the composition of the gill-net fleets only the years 1961—64 and 1966—68 can be used to estimate the natural mortality. Only fish that were 27 cm or bigger when tagged were included in the estimates.

The estimated survival rates and their 95 % confidence intervals are shown in Table 19. If fishing and natural mortality are evenly distributed through the whole year, F and M can be estimated when S and E (the rate of exploitation) are known. As we know nothing about the distribution in time of the natural mortality, we will assume that it operates at a constant rate throughout the year. The fishing mortality, however, is only working in three—four summer months. As the exact distribution in time of the recaptures is known, M can be estimated by iterations on the computer according to the method described by REGIER (1962). The resulting estimates of M are shown in Table 19. Our best estimate of M is the geometric mean of these seven $\widehat{M}$-values, which is $\widehat{M}=0.31$.

As the confidence intervals for $\hat{S}$ are broad, the statistical uncertainty of M is substantial. There are also the possibilities of seasonal variations in natural mortality, of variations in M correlated to size or age, of great differences in M from year to year, etc. Our estimate is obviously in need of comparision with mortality estimates from other trout lakes, and we should also try to obtain survival estimates by methods that are independent of tagging.

Natural mortality in wild trout populations was estimated by the author in two Norwegian lakes: Olavatn and Songsjøen. The same methods

Table 18. *Recaptures (in percent) from tagging experiments.*

Year of tagging	≦ 26 cm							> 26 cm						
	No. tagged	Recapt. year 1 %	Recapt. year 2 %	Recapt. year 3 %	Recapt. year 4 %	Later recapt. %	Total %	No. tagged	Recapt. year 1 %	Recapt. year 2 %	Recapt. year 3 %	Recapt. year 4 %	Later recapt. %	Total %
1958	46	13	13	13	2	2	43	46	33	24	2	—	—	59
1959	20	10	30	5	5	—	50	22	27	27	—	—	—	55
1960	32	25	19	9	—	—	53	14	29	21	7	—	—	57
1961	105	30	16	13	—	—	59	109	56	15	8	—	—	79
1962	41	20	22	10	—	2	54	57	53	19	7	—	5	84
1963	51	29	24	10	—	—	63	58	52	14	12	3	—	81
1964	72	28	10	7	—	—	44	38	39	24	13	—	3	79
1965	85	22	21	9	2	—	55	95	55	25	2	1	—	83
1966	91	26	25	2	—	—	54	126	40	17	6	2	3	69
1967	94	35	22	4	—	1	63	107	47	25	1	2	—	75
1968	80	50	16	3	5	—	74	99	57	11	4	1	—	73
1969	117	57	11	13	1	—	82	107	44	21	15	3	—	82
1970	125	30	28	11	—	—	(70)	177	27	41	10	—	—	(78)
1971	128	28	23	—	—	—	—	166	49	22	—	—	—	—
1972	159	35	—	—	—	—	—	135	39	—	—	—	—	—

Table 19. *Estimates of survival and natural mortality.*

Year	m_1	R_{11}	R_{12}	$\hat{S}$	$\widehat{M}$	95 % conf. int. for $\hat{S}$
Ø. Heimdalsvatn						
1961	109	61	16	0.2699	0.37	0.11—0.43
1962	57	30	11	0.3611	0.23	0.11—0.61
1963	58	30	8	0.3276	0.32	0 —0.71
1964	38	15	9	0.4245	0.32	0.12—0.73
1966	126	50	22	0.3663	0.44	0.18—0.55
1967	107	50	27	0.4383	0.16	0.24—0.64
1968	99	56	11	0.2477	0.43	0.08—0.41
1969	107	47	—	—	—	—
Olavatn						
1969	159	64	42	0.4723	0.21	0.29—0.66
1970	118	65	—	—	—	—
Songsjøen						
1968	300	150	46	0.2848	0.47	—
1969	299	146	48	0.3294	0.36	—
1970	296	157	—	—	—	—

were used as in Ø. Heimdalsvatn. The results from Olavatn were described by Jensen (1972).

Songsjøen (altitude 265 m) is situated in Snillfjord in Sør-Trøndelag, and the only fish species are brown trout and char (*Salvelinus alpinus*, L.). Fishing was completely controlled in 1968—70. As gill nets with meshes down to 24 mm were used for recapture all tagged trout regardless of size have been included in the mortality estimates. In Songsjøen in 1969 the fishing was done about four months after the 1969-tagging was completed, and this will bias survival estimates from formula (9). To avoid this kind of error, M was estimated by using trial values for $\widehat{M}$ and calculate $\hat{m}_1$ as the number of surviving tagged fish after four months exposure to this natural mortality alone. $\hat{m}_1$ was then used in formula (9) to estimate S. The next step was to use $\hat{S}$ to estimate the number of surviving tagged fish at the date of the 1970-tagging. The acceptability of the trial value for $\widehat{M}$ and the associated $\hat{S}$ was then controlled graphically by Regier's method and iterations. As the values for m_2 in 1968 and m_1 in 1969 are estimated figures, formula (5.3) in Ricker (1958) would underestimate the variance of $\hat{S}$. Confidence intervals for $\hat{S}$ are therefore not given.

The estimates from Olavatn and Songsjøen are also included in Table 19. The magnitude of M in these two lakes may well be about the same as in Ø. Heimdalsvatn.

C. *Survival estimates from age composition*

As total mortality is one of the factors determining the age composition in a fish stock, the age composition can be used to estimate survival rates. However, variations in year-class strength, difficulties in securing representative samples and other sources of error can seriously bias the results.

Where material from a succession of years is available, the errors caused by variations in year-class strength can be avoided by studying each year-class separately. Better still, we can under certain conditions estimate the total mortality rate from the virtual populations.

When the fishing effort is varying substantially from year to year, the natural mortality can be estimated by extrapolation of the regression line of the logarithm of virtual population upon fishing effort, but as shown by Bishop (1959) the results are biased.

Provided that both fishing and natural mortality do not vary from year to year the biostatistical method can be used to obtain unbiased estimates of the total mortality rate (Ricker 1971). The ideal situation where there is no variation in the fishing mortality through a sequence of years is never found, and usually very little is known about eventual variations in the natural mortality. Probably the natural mortality is increasing with age among trout above a certain age. However, even an increase in M of 20 % per year will only make the biostatistical rate of exploitation (C/V) about 5 % larger than the true rate of total mortality, and also the changes in F found in most situations will give only small errors (RICKER 1971).

By the biostatistical method the total mortality rate, A, is estimated from the equation

$$\hat{A} = C/V$$

where C is the catch in a certain year and V the virtual population in the same year. Only for fully recruited year-classes is C/V an unibiased estimate of A, and we shall therefore use only trout that were 7 years or more in 1961—62 and 6 years or more from 1963. After 1966 the virtual population of 6 and 7 years old fish can not be calculated as these year-classes have not yet been fished to extinction.

In Table 20 the survival rates as estimated by tagging are compared with the survival rates estimated by the biostatistical method. The rates estimated by the last method are all within the (admittedly wide) 95 % confidence intervals of the same rates estimated by means of tagging, and the arithmetic means of the two groups of estimates are nearly the same. As the two groups of estimates are independent of each other, this indicates that our survival estimates from tagging can not be consistently wrong to any large extent, and this increases our confidence that our estimate of the average value for M is of the right magnitude.

VIII. ESTIMATES OF POPULATION NUMBER, BIOMASS AND DENSITY

The simple and commonly used method that was later called the PETERSEN method, was first used by DAHL (1917) to estimate the number of trout present in small lakes. As he used a small-meshed seine, fin-cutting for marking and continued fishing and marking until he after a few days had obtained a sufficient number of recaptures, his estimates were probably not biased by recruitment or differences in catchability between marked and unmarked fish.

Table 20. *Rates of survival estimated from tagging and by the biostatistical method.*

Year	$\hat{S}$ (from tagging)	$\hat{S}$ (from the b.st. method)
1961	0.27	0.29
1962	0.36	0.25
1963	0.33	0.31
1964	0.42	0.34
1966	0.37	0.48
Mean	0.350	0.334

The PETERSEN method can be used also to estimate the number of trout present in Ø. Heimdalsvatn in the different years. However, variations in catchability associated with trout size and the effects of recruitment during the fishing season will make the reliability of PETERSEN estimates very doubtful. A more promising approach is to estimate the true populations from the virtual populations.

A. *Population estimates based on virtual populations*

FRASER (1955) used data from tagging to convert virtual population estimates to estimates of actual populations. Unfortunately one of the assumptions of his method is a constant rate of tag loss through the whole life-span of the fish, and in our case this is improbable.

PALOHEIMO (1958) showed for virtual populations how "with an almost obvious modification, we may obtain correct estimates of the size of a year-class if the fishing and natural mortality are known" (*loc.cit.* p. 750). As stated by WATT (1968, p. 210) "it is possible to combine the basic idea of the virtual population technique with certain ideas from other techniques and arrive at a procedure that is very powerful indeed".

Let us consider the problem: For the year-classes into which no immigration took place at a later date, the virtual populations shown in

Table 15 are minimum estimates of the number of trout present in the lake at each year's start of the fishing season. For a year-class which was fished to extinction we could estimate its abundance in previous years by successive use of PALOHEIMO's formula:

$$N_i = N_{i+1} + (F_i + M_i) \cdot C_i / F_i \qquad (10)$$

where N_i is the number of fish of age i at the start of the year, C_i is the number of fish of age i in the catch, and F_i and M_i are the instantaneous mortality coefficients for fish of age i. Estimates of F based on the virtual populations will be biased (BISHOP 1959).

If we try to estimate F from the rate of exploitation of the tagged fish, we meet the difficulty that the fishing mortality is not evenly distributed through the year. Better, therefore, in our case, to avoid PALOHEIMO's formula, but still use the basic principle of his method, *viz.* to build up the year-classes from the virtual populations. We can do this by using the average value $\widehat{M}=0.31$ from the tagging experiments and combine this natural mortality with the actual numbers of trout that each month were killed by fishing. How these data can be used to build up the year-classes is best shown by an example:

To the yearly coefficient $M=0.31$ corresponds a monthly coefficient of 0.02583 if the natural mortality rate is constant through the year. In a month when there was no fishing we have:

$$N_1 = N_0 \cdot e^{-0.02583}$$

where N_0 is the number of fish of a certain year-class on the first day in the month and N_1 is the number of survivors one month later. If N_1 is known, we can therefore backcalculate N_0 as:

$$N_0 = N_1 \cdot e^{0.02583} = N_1 \cdot 1.026. \qquad (11)$$

Still one month earlier the number of individuals in the year-class would be: $N_1 \cdot 1.026^2$, and in this way we can continue in all months without fishing. In a month when fishing was done, we follow the same procedure, but add the number of fish belonging to the year-class which was caught in that month. By this method we do not take in account the interaction between natural and fishing mortalities in the few months of the years (before 1969) when fishing took place. In these months our figures for natural mortality will be a little too high. This will tend to make our population estimates too high, but as we shall see, gross errors in $\widehat{M}$ are needed to give serious errors in the population estimates.

In order to use this method we must know the approximate monthly distribution of the catch of each year-class through its whole life. This was estimated by giving each month's total catch the same age distribution as that found in the scale samples from the same month. Usually the July samples were too few to make this possible for the July catch, and fish caught in July were given the same age distribution as those caught in August. As the July catches were small the possible error from this is of small consequence.

From practical reasons the number of fish caught during one month were treated as if they had all been caught on the last day of the month. Errors in year-class build-up caused by this simplification are negligible. Trial runs on the computer showed that even if all fish caught during the months July—September were treated as caught on 15 August, the error caused by this would be of small consequence.

The consequence of errors in our estimate of M must be considered. M is probably varying from season to season, from year to year and between age groups. Our $\widehat{M}=0.31$ is only an estimated average value. However, because of the high fishing mortality, errors in the estimates of natural mortality will not give errors of a corresponding magnitude in the population estimates. In order to obtain an impression of the size of the errors involved, the year-classes were built up with $M=0.155$ and with $M=0.465$. If $M=0.155$ were the true coefficient our estimate of $\widehat{M}=0.31$ would be 100 per cent too high. Still the error in the year-class estimates would be of the magnitude of only 5 per cent for nine-year-old fish, 10 per cent for seven-year-olds, 30 per cent for five-year-olds and 45 % for four-year-old fish. If true M were 0.465, or 50 per cent higher than our estimate, our $\widehat{M}=0.31$ would give an error of approximately 5 per cent for nine-year-old fish, 10 per cent for eight-year-olds and 35 per cent for four-year-old fish. Changes in M of a reasonable magnitude during the exploited phase of year-class — for instance from

Table 21. *Estimated year-class abundance on 1 June ($\hat{M}=0.31$).*

Year	Year-class											
	1946	—47	—48	—49	—50	—51	—52	—53	—54	—55	—56	—57
1958	16	17	176	1074	1786	2254	2649	3338	5048	5263	—	—
1959	1	1	28	267	639	1174	1768	2418	3596	3857	3263	—
1960	—	—	7	108	286	496	959	1511	2486	2775	2387	4504
1961	—	—	4	14	103	155	312	585	1271	1765	1649	3304
1962	—	—	3	6	36	29	70	145	394	724	928	2149
1963	—	—	—	—	9	8	10	36	98	189	401	1168
1964	—	—	—	—	1	2	1	1	16	58	119	389
1965	—	—	—	—	—	1	—	—	2	8	41	138
1966	—	—	—	—	—	—	—	—	—	2	20	28
1967	—	—	—	—	—	—	—	—	—	1	4	9
1968	—	—	—	—	—	—	—	—	—	1	—	1
1969	—	—	—	—	—	—	—	—	—	1	—	—
1970	—	—	—	—	—	—	—	—	—	—	—	—
1971	—	—	—	—	—	—	—	—	—	—	—	—
1972	—	—	—	—	—	—	—	—	—	—	—	—
1973	—	—	—	—	—	—	—	—	—	—	—	—

Year	Year-class										
	—58	—59	—60	—61	—62	—63	—64	—65	—66	—67	—68
1958	—	—	—	—	—	—	—	—	—	—	—
1959	—	—	—	—	—	—	—	—	—	—	—
1960	—	—	—	—	—	—	—	—	—	—	—
1961	3073	—	—	—	—	—	—	—	—	—	—
1962	2207	6494	—	—	—	—	—	—	—	—	—
1963	1540	4702	7807	—	—	—	—	—	—	—	—
1964	823	2985	5698	(5460)	—	—	—	—	—	—	—
1965	279	1401	3792	(3983)	(3466)	—	—	—	—	—	—
1966	90	584	2288	(2806)	(2536)	?	—	—	—	—	—
1967	38	232	1013	(1635)	(1758)	?	?	—	—	—	—
1968	7	44	301	(729)	(1052)	?	?	?	—	—	—
1969	—	2	32	(179)	(478)	?	?	?	?	—	—
1970	—	—	11	(47)	(204)	?	?	?	?	?	—
1971	—	—	3	(16)	(59)	?	?	?	?	?	?
1972	—	—	—	(4)	(21)	—	—	—	—	—	—
1973	—	—	—	—	(5)	—	—	—	—	—	—

M=0.465 for nine-year-old fish and gradually decreasing to M=0.155 for four-year-olds — would not give serious errors in the built-up year-classes.

By this method year-classes that were fished to extinction were built up, beginning with the time when the last individual(s) of the year-class appeared in the catch. The results are shown in Table 21.

In the years after 1963 we can not use this method to estimate the total population present in the lake, because some of the year-classes involved have not yet been exterminated. However, the year-classes 1961 and 1962 are obviously so reduced that we can "guesstimate" the number of survivors in 1972 without risking more than minor errors in the build-up of year-classes. The figures of four 11-year-old and 21 10-year-old fish in 1972 were used. From these figures the year-classes 1961 and 1962 were built up in the usual way. The results are given in brackets.

As a check on the reliability of Petersen estimates based on Carlin-tagged trout, Petersen estimates corrected for recruitment were compared with estimates obtained by the biostatistical method (JENSEN 1974).

There was good agreement between the two sets of figures. Five of the PETERSEN estimates were smaller than the biostatistical estimates and eight were bigger. In seven of the comparisons the difference between the two kinds of estimates was 10 per cent or smaller, and the greatest difference was only 26 per cent. One of the biostastistical estimates was outside the 95 per cent confidence range of the PETERSEN estimate, but this is not alarming when 13 comparisons are involved.

For the age groups 4 years and older we have now complete estimates for the years 1958—66. For the years 1967—71 an increasing number of age groups can not be estimated by this method, but we can try to obtain estimates from observations of catches per unit of fishing effort.

B. Population estimates from catch/effort data

When the fishing mortality is of a sufficient magnitude to cause a rapid decrease in the size of the exploited part of the population, data of catch per unit of fishing effort (C/E-data) can be used for population estimates. The principle was used on trout by I. D. SØMME (1934 p. 585) to estimate the exploited population in some small lakes on Hardangervidda. Important improvements in the method were introduced by LESLIE and DAVIS (1939), DE LURY (1947) and others, and it is commonly referred to as DE LURY's method.

Unfortunately DE LURY's method is of little use in our case. Some of the reasons are that the catchability of the trout is increasing during the fishing season and at the same time immigration takes place into the young age groups. Commonly the catch per unit of effort is increasing towards the end of the fishing season. Besides, the great variations in catchability with weather, moon etc. give difficulties.

However, the *yearly* average catches per unit of fishing effort can be tried as indices of population abundance. We shall first compare C/E-values with the estimated population figures for the same years.

The changes in the composition of the fleet of gill-nets and the great changes in growth rates after 1958 have caused great variation from year to year in the vulnerability of the different age groups. This was clearly seen from plots of the yearly catches of fish of a certain age against total yearly fishing effort. Therefore only the catches taken on the pilot nets with their wide and unchanged range of mesh size have been used. These catches, the total effort (number of gill-net nights) and the catch per 10 gill-net nights (C/E×10) are shown in Table 22. In the same table are shown the biostatistical population estimates primo June taken from Table 21.

For each age the biostatistical population estimates for the years 1959—70 were plotted against the C/E-values in the manner shown for the 6-year-old fish in Fig. 7. For most ages the C/E-values for 1959 were obviously too small. The main reason is probably that in 1959 and in July 1960 the nets were usually standing on the same place for two nights or more, although they were lifted daily and the catch taken away. From August 1960 on, and in all later years, the nets were moved to new places every day. After 1960 the pilot nets were only used in August, September and the beginning of October, when the catches usually are better than in July. The year 1959 and July 1960 were therefore excluded from the calculations.

Ordinary linear regressions (predictive regressions) of the age groups 4—9 gave r-values between 0.65 and 0.96. However, RICKER's GM regression is probably a more appropriate measure of the functional relationship between these variables. The GM regressions were therefore computed. The approximate confidence intervals for the slope, v, of the GM regression lines were computed from expression (6).

The population estimates in 1967—70 that are missing in Table 22 can now be computed by means of the GM regressions and the C/E-values. The computed estimates and their 95 % confidence intervals are shown in Table 23.

As the pilot nets were not used in 1971, we can not use C/E to estimate the trout population in that year. Estimates from tagging—recapture (PETERSEN estimates) corrected for recruitment were tried, but apparently these under-estimated the young age groups. One reason for this is that the

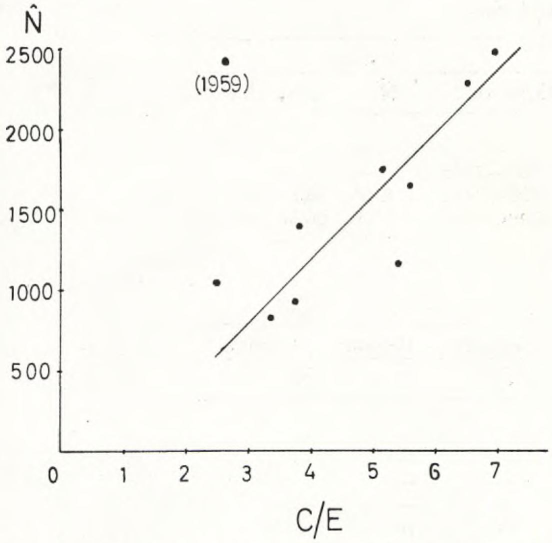

Fig. 7. GM-regression of estimated numbers of 6-years trout on corresponding C/E figures.

biostatistical estimate of, for instance, 4-years old fish on 1 June 1961 include also later immigrants to the lake of that year-class. Another reason is that probably the attached tag substantially increases the vulnerability to the gill nets of the small fish. A trout which is small enough to pass through a mesh may more easily be hanging in the tag than a trout of modal length or bigger.

We shall therefore abandon the PETERSEN method and instead use the 1970-estimate to estimate the 1971 population by means of the estimated average natural mortality and the observed numbers of individuals killed by fishing for each age group for each month. The resulting estimate for 1971 is included in Table 23.

An estimate of 4-year-old fish in 1971 is still missing.

C. *Population biomass and density*

The biomass at the time t of a year-class of trout can be estimated by multiplying the estimated number of fish with their estimated mean weight at the time t: ($\hat{B}_t = \widehat{N}_t \times \hat{\hat{w}}_t$).

The individual weight at the beginning of the growth season can be estimated by conversion to weight of the individual back-calculated length

Table 22. *Catch/Effort on the pilot nets.*

Year	Effort	4 years old			5 years old			6 years old			7 years old			8 years old			9 years old		
		Catch	C/Ex 10	Pop. est.	Catch	C/Ex 10	Pop. est.	Catch	C/Ex 10	Pop. est.	Catch	C/Ex 10	Pop. est.	Catch	C/Ex 10	Pop. est.	Catch	C/Ex 10	Pop. est.
1959	120	7	0.58	3857	22	1.83	3596	32	2.67	2418	48	4.00	1768	52	4.33	1174	30	2.50	639
1960	96	17	1.77	2387	55	5.73	2775	67	6.98	2486	39	4.06	1511	19	1.98	959	19	1.98	496
1961	112	37	3.30	3304	32	2.86	1649	58	5.18	1765	41	3.66	1271	33	2.95	585	16	1.43	312
1962	96	21	2.19	2207	99	10.30	2149	36	3.75	928	31	3.23	724	23	2.40	394	10	1.04	145
1963	120	93	7.75	4702	47	3.92	1540	65	5.42	1168	13	1.08	401	16	1.33	189	5	0.42	98
1964	104	72	6.92	5698	91	8.75	2985	35	3.37	823	27	2.60	389	7	0.67	119	1	0.10	58
1965	112	32	2.86	(3983)	102	9.11	3792	43	3.84	1401	10	0.89	279	6	0.54	138	0	0	41
1966	136	43	3.16	(2536)	89	6.54	(2806)	89	6.54	2288	17	1.25	584	2	0.15	90	1	0.07	28
1967	128	19	1.48	—	67	5.23	(1758)	72	5.63	(1635)	49	3.83	1013	13	1.02	232	1	0.08	38
1968	120	33	2.75	—	43	3.58	—	30	2.50	(1052)	31	2.58	(729)	15	1.25	301	4	0.33	44
1969	104	34	3.27	—	39	3.75	—	46	4.42	—	18	1.73	(478)	14	1.35	(179)	1	0.10	32
1970	88	45	5.11	—	70	7.95	—	31	3.52	—	18	2.05	—	9	1.02	(204)	0	0	(47)

Table 23. *Population estimates based on C/E data.*

Year	4-years		5-years		6-years	
	$\widehat{N}$	95 % conf.int.	$\widehat{N}$	95 % c.i.	$\widehat{N}$	95 % c.i.
1967	2127	1637—2618	—	—	—	—
1968	2845	1933—3756	1532	709—2355	—	—
1969	3139	2055—4222	1584	722—2446	1355	560—2151
1970	4178	2484—5872	2856	1028—4683	1000	367—1634
1971	—	—	2938	—	1744	—

Year	7-years		8-years	9-years	10-years	11-years
	$\widehat{N}$	95 % c.i.	$\widehat{N}$	$\widehat{N}$	$\widehat{N}$	$\widehat{N}$
1967	—	—	—	—	—	—
1968	—	—	—	—	—	—
1969	—	—	—	—	—	—
1970	586	283—890	—	—	—	—
1971	528	—	258	58	16	3

when the corresponding annulus was completed. When *average* lengths shall be converted to *average* weights the "year-class b" (Ricker, 1958, 1969) must be used.

Let us now use an example to examine the probable effects of the size-selective mortality. We can use $\bar{l}_4$ for the four-year-old trout caught in 1960 and "year-class b" to estimate the mean weight in June 1960 of trout belonging to the year-class 1956. This method (method A) will probably give a too high $\bar{w}_4$ because $\bar{l}_4$ is too high, as is indicated by the positive Lee's phenomenon. However, survivors from year-class 1956 were caught in many years after 1960, and their individual l_4 can be back-calculated and converted to individual weights by means of the coefficients in Table 10 and then averaged. We shall call this procedure method B.

Method B was preferred and used on all fish in the material 1958—70. As expected, the mean weights computed in this way were usually smaller than the means computed by method A, especially for the youngest groups. For the estimates of the population biomass this is not so important;

Table 24. *Estimated biomass (kg) and density (kg/ha) of trout on 1 June.*

Year	Age											Biomass	Density
	4	5	6	7	8	9	10	11	12	13	14		
1958	207.5	234.0	278.1	301.4	267.7	181.0	32.8	3.3	4.6	—	—	1510.4	19.5
1959	140.0	252.4	255.6	259.9	205.8	122.5	55.9	7.3	0.2	0.4	—	1300.0	16.8
1960	87.1	187.3	282.7	226.5	175.3	105.4	67.2	29.1	2.1	—	—	1162.7	15.0
1961	125.6	117.7	194.3	206.5	115.7	71.6	39.3	29.0	4.4	1.4	—	905.5	11.7
1962	91.8	174.3	116.7	121.1	82.1	38.5	19.9	9.0	12.2	3.0	1.3	669.9	8.6
1963	189.0	121.5	144.8	80.8	44.7	29.5	15.4	3.4	2.9	4.8	—	636.8	8.2
1964	222.2	268.1	125.9	87.8	40.3	19.1	6.2	0.4	0.5	0.6	1.1	772.2	10.0
1965	149.0	325.7	233.3	71.1	45.3	20.0	3.9	1.8	—	—	0.9	851.0	11.0
1966	90.3	217.2	316.2	125.6	28.7	10.7	13.3	0.9	—	—	—	802.9	10.4
1967	73.0	129.9	231.0	201.9	60.5	11.5	4.4	2.4	0.5	—	—	715.1	9.2
1968	115.2	112.6	139.2	149.4	80.1	14.7	3.7	1.2	—	0.6	—	616.7	8.0
1969	151.3	166.0	221.9	111.7	55.0	12.6	1.1	—	—	—	0.6	720.2	9.3
1970	326.3	354.7	188.4	164.4	68.5	20.1	6.0	—	—	—	—	1128.4	14.6

method A gives only about 5—10 per cent higher values than method B for the total biomass of the age groups 4—14 years.

The biomass of trout from four years and older can now be estimated and the results are shown in Table 24. The last column in the table gives the estimated density in kg per ha.

IX. THE DEPENDENCE OF TROUT GROWTH ON POPULATION DENSITY AND TEMPERATURE

A. Growth and population density

The density dependence of growth in fishes is a well documented fact. That the growth of brown trout can be closely related to the size of the trout population was early shown by DAHL (1917). Unfortunately this was often forgotten when later authors studied the influence of acidity or other abiotic factors on trout growth.

Substantial changes in fishing mortality will change the density of the exploited trout population and can by this cause substantial changes in the growth rates. Realistic models for predicting trout yields at different levels of fishing mortality must therefore incorporate the density dependence of growth.

In RICKER's yield model (RICKER 1958) the growth is exponential and described by the coefficient G which is changing during the individual's life. The G-values for a certain time period must be calculated separately for each age group. Unfortunately there is no law or rule that can be used to predict G for trout of age (n+1) if G is known for trout of age n. The relationship between the G-values and the population density must therefore be described with a new equation for each age. There is a possibility that VON BERTALANFFY's growth equation can give a simpler description of the density dependence of trout growth, and we shall examine this possibility.

In VON BERTALANFFY's equation:

$$l_t = L_\infty(1 - e^{-K(t-t_0)}) \tag{12}$$

the length at the time t is described by the three parameters L_∞, K and t_0. BEVERTON and HOLT (1957 p. 107) suggest that the value of the parameter K does not vary greatly even over a wide range of food consumption. Therefore the trout growth at different population densities could possibly be described by changes in L_∞ only. If this is so, an equation relating L_∞ to population density could solve our problem. In order to examine this possibility WALFORD lines (WALFORD 1946) were computed for the trout growth in each of the years 1958—70 and L_∞ determined as the intersection between the WALFORD line and the 45° line. K was computed as $-\log_e b$, where b is the slope of the WALFORD line. Finally W_∞ was calculated from L_∞ by means of the predictive regression coefficients given in Table 10.

These computations were first done on the uncorrected mean lengths at successive ages. The results are shown in the last four columns in Table 25. Columns 2—5 in the same table show the results of the same computations done on growth data corrected for size-selective mortality by the method suggested by RICKER (1969). Here the WALFORD lines were computed for the points L/L_c where L was the back-calculated lengths at the last annulus (age n) and L_c the back-calculated length at age (n—1).

As seen from the tabulated correlation coefficients (r) the corrected data give the best fits to WALFORD lines. L_∞ and W_∞ are of a reasonable magnitude when calculated from the corrected figures, while they attend impossible dimensions from the uncorrected data for 1963 and 1966.

Whether the growth data are corrected or not there is considerable variation from year to year in *both* L_∞ and K. Although yearly variation in temperature and probably also other factors besides population density influence the growth and obscure the picture, there is no doubt that in 1958 when the trout density was high and the growth correspondingly slow, L_∞ (and W_∞) were low and K was high. As the growth improved in later years L_∞ (and W_∞) increased substantially and K decreased substantially. A plot of K against L_∞ indicates a negative correlation between these parameters, but the scatter of the points is too great to make a further analysis promising.

Doubts about the consistency of the relationship between K and L_∞ or W_∞ have been raised by previous authors. CUSHING (1968, p. 105) found

Table 25. L_∞, W_∞ *and K for corrected and uncorrected growth data.*

Year	Corrected growth data				Uncorrected growth data			
	L_∞ (mm)	W_∞ (gram)	K	r	L_∞	W_∞	K	r
1958	287.79	223	0.4530	0.99582	265.35	176	0.4752	0.91825
1959	355.77	433	0.2112	0.99946	324.84	344	0.2311	0.96929
1960	365.51	484	0.2238	0.99913	344.86	405	0.1972	0.99532
1961	362.12	488	0.2554	0.99945	341.69	406	0.1999	0.99340
1962	367.71	499	0.2734	0.99882	408.26	690	0.1229	0.99759
1963	519.47	1600	0.1049	0.99944	1077.51	15800	0.0320	0.99055
1964	504.55	1520	0.1811	0.99533	382.01	630	0.1978	0.98145
1965	545.36	1947	0.1731	0.99946	421.46	849	0.2057	0.99891
1966	581.64	2246	0.1208	0.99982	−208.48	—	−0.0893	0.99340
1967	397.14	705	0.1148	0.98736	327.43	377	0.3456	0.98447
1968	435.62	964	0.1703	0.99911	401.58	744	0.1675	0.99272
1969	448.98	1048	0.2323	0.99888	408.95	783	0.1953	0.99515
1970	492.39	1265	0.2283	0.99894	566.69	1958	0.1015	0.99135

no relationship between K and W_∞ in different year-classes of the Downs' stock of the North Sea herring and concluded: "It is possible that the growth processes summarized by the two growth constants vary independently to some degree."

The parameter L_∞ has a certain physiologic meaning as it shows the maximum length that can be obtained if the growth is accurately described by the WALFORD line. This "physiologic meaning" is of course implicit in the definition of L_∞ as the point on the WALFORD line where $l_{t+1}=l_t$. For the same fish species L_∞ can vary very much from place to place and from time to time depending on factors as temperature, access to food etc. The parameter K has no proven physiologic meaning and, as we have seen, even within a discrete population of trout pronounced variations in K can quickly take place when the growth rates change. In the author's opinion VON BERTALANFFY's equation is only one of the numerous models that can be fitted to growth data when three parameters are calculated from the data. Only accuracy and convenience should be the criteria for evaluating models of this kind. As both L_∞, K (and also t_0) change with trout population density, the model promises no obvious advantage for predictions of growth rates at varying levels of population density. We shall therefore proceed with the simple exponential growth model.

B. *Growth and temperature*

For brown trout the dependence of growth on temperature has been well demonstrated in laboratory experiments (BROWN 1946, SWIFT 1955). Also for free-living populations of brown trout the influence of temperature on growth has been shown. One of the first authors to study this was HUITFELDT-KAAS (1913, 1927) who found that the trout in lakes Tyin and Nedre Leirungen had a better growth in summers with high air tempetatures than in cold summers. However, his material was small, and S. SØMME (1930) could not confirm his results on another small material from Lake Tyin. Later authors have shown beyond doubt that in Scandinavian mountain lakes the trout growth can be positively correlated to the summer temperature (RUNNSTRÖM 1957, STUBE 1958).

We shall see that also in our lake the trout growth is significantly influenced by the summer temperature. As we are mainly interested in the connection between growth rates and population densities, we must try to separate the variance due to temperature variation.

C. *Growth as a function of summer temperature and trout population density*

Unfortunately the water temperatures in the lake have only been observed in the last years. However, as the lake is not fed by glaciers we can assume that when the lake is ice-free there will be a positive correlation between the mean air temperature and the water temperature. The nearest meteorological station with a sufficiently long series of air temperature measurements is Vågåmo (61°52'N, 9°6'E, 371 m above the sea level) which is situated about 52 km NNE of our lake. The mean monthly air temperatures at Vågåmo in June—September are given in Table 26. The data were furnished by The Norwegian Meteorological Institute.

Fig. 8 shows the population density (D), G_4—G_9 and the mean air temperature at Vågåmo in June (T_6) and for June—september (T_m) for the years 1958—70. Apparently there is a strong positive correlation between the different G-values in the same year. This is confirmed by Table 27 which shows the computed correlation coefficients, the t-values and the probability of larger values of t. However, between G_9 and the other G-values no significant correlation was found, probably because the G_9-values were based on too few observations.

The correlations between G and the monthly temperature means are shown in Table 28. G_4, G_5 and G_6 are positively correlated to the June mean, but no significant correlation was found between G-values and the other monthly temperature means. Neither was G correlated to the mean summer temperature, T_m (calculated as $(T_6+T_7+T_8+T_9)/4$). This was rather unexpected. One possible explanation is that good growth is mainly depending on an early start of the growth season and a high June temperature will tend to give an early break-up of the ice on the lake.

The last rows in the table show the correlation between the G-values and the population densities (D). G_5, G_6 and G_7 are negatively correlated to D. The negative correlation between G_4 and D is not significant. The reason for this may be that a high proportion of 4-year-old fish are still living in the nursery streams where their access to food is not directly influenced by the trout density in the lake.

Multiple linear regressions were computed with G as the dependent variable and T_6 and D as independent variables. The results are shown in the upper half of Table 29. G_4—G_7 can be estimated quite well from equations of the form:

$$G_n = a + b_{y1.2} \cdot T_6 + b_{y2.1} \cdot D \qquad (13)$$

but for G_8 the regression is not significant. The standard partial regression coefficients ($b'_{y1.2}$ and $b'_{y2.1}$) are of approximately the same size. This indicates that June temperature and population density have approximately the same effectivity as predictors of growth coefficients.

However, equation (13) predicts that if the

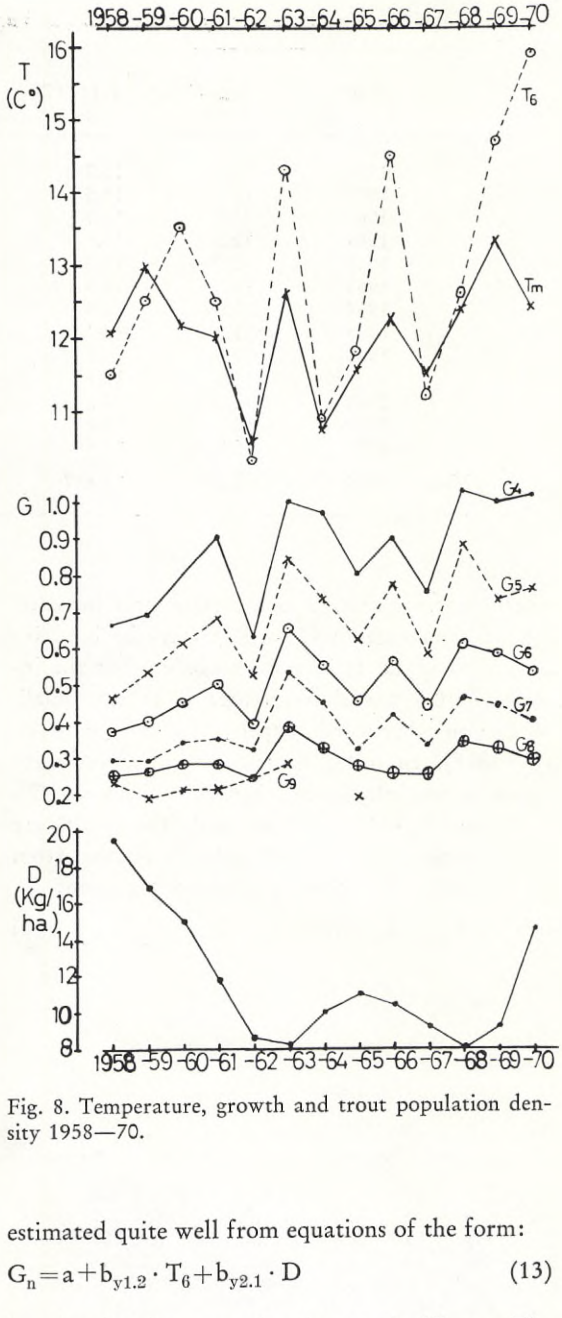

Fig. 8. Temperature, growth and trout population density 1958—70.

Table 26. *Monthly air temperature means at Vågåmo.*

	Year	June (T6)	July (T7)	August (T8)	September (T9)	Mean June—September (T_m)
	1958	11.5	13.2	13.0	10.5	12.050
	1959	12.5	15.5	14.2	9.7	12.975
	1960	13.5	13.3	13.3	8.5	12.150
	1961	12.5	13.6	11.5	10.4	12.000
	1962	10.3	13.0	11.1	7.9	10.575
	1963	14.3	14.3	13.5	8.3	12.600
	1964	10.9	11.9	12.3	7.8	10.725
	1965	11.8	12.7	12.2	9.5	11.550
	1966	14.5	14.3	12.2	8.1	12.275
	1967	11.2	13.1	12.8	8.9	11.500
	1968	12.6	13.7	13.9	9.3	12.375
	1969	14.7	14.1	16.1	8.4	13.325
	1970	15.9	12.5	13.6	7.6	12.400
Mean	1958—70	12.785	13.477	13.054	8.838	12.039

mean june temperature in a certain year increases 1°C, the increase in G_n will always be $b_{y1.2}$ independent of D. It is more probable that the increase in G_n would be greater if D was small. We can, in other words, expect interaction between T_6 and D. In order to examine this possibility step-wise mutiple linear regressions between G_n, T_6, D and $T_6 \cdot D$ were computed. The results are shown in the lower half of table 29. As seen from the increase in R^2 and t equations of the form:

$$G_n = a + b_{y1.2} \cdot T_6 + b_{y2.1} \cdot T_6 \cdot D \qquad (14)$$

will give better estimates of G-values than equation (13).

Observations from pond culture of carps (Hepher 1967) and from trout fry in screened portions of small streams (Le Cren 1965, 1972, Backiel and Le Cren 1967) indicate within certain limits negative proportionality between growth rates and the logarithms of population densities. Therefore the models:

$$G_n = a + b \cdot T_6 + c \cdot \log D + d \cdot T_6 \cdot \log D \qquad (15)$$

and

$$G_n = a + b \cdot T_6 + c \cdot T_6 \cdot \log D \qquad (16)$$

were examined by step-wise multiple linear regressions but found less efficient than model (14).

We shall therefore in the following computations use model (14) to predict the influence on the growth by variations in temperature and population density. The original G-values (from Table 11) and the G-values predicted by the model are shown in Table 30.

Table 27. *Correlation between pairs of G-values 1958—70.*

X_1	X_2	N	r	t	Probability of larger t
G_4	G_5	13	0.94	9.34	$P < 0.001$
G_4	G_6	13	0.93	8.71	$P < 0.001$
G_4	G_7	13	0.87	5.81	$P < 0.001$
G_4	G_8	13	0.79	4.27	$P = 0.001$
G_4	G_9	7	0.38	0.91	$0.4 < P < 0.5$
G_5	G_6	13	0.97	13.39	$P < 0.001$
G_5	G_7	13	0.91	7.24	$P < 0.001$
G_5	G_8	13	0.78	4.16	$0.001 < P < 0.01$
G_5	G_9	7	0.50	1.28	$0.2 < P < 0.4$
G_6	G_7	13	0.97	12.23	$P < 0.001$
G_6	G_8	13	0.85	5.30	$P < 0.001$
G_6	G_9	7	0.60	1.67	$0.1 < P < 0.2$
G_7	G_8	13	0.89	6.39	$P < 0.001$
G_7	G_9	7	0.78	2.80	$0.02 < P < 0.05$
G_8	G_9	7	0.65	1.92	$0.1 < P < 0.2$

X. YIELD ESTIMATES

Jensen (1972) estimated sustained yields from a trout lake at varying fishing efforts, but with fixed growth rates. We shall now try a more elaborate model on the trout in Lake Ø. Heim-

Table 28. *Correlation between G-values, summer temperatures, and population densities. 1958—70.*

Y	X	N	r	t	Probability of larger t
G_4	T_6	13	0.64	2.75	$0.01 < P < 0.02$
G_4	T_7	13	−0.082	0.27	
G_4	T_8	13	0.39	1.39	
G_4	T_9	13	−0.37	1.34	
G_4	T_m	13	0.34	1.20	
G_5	T_6	13	0.58	2.34	$0.02 < P < 0.05$
G_5	T_7	13	0.04	0.13	
G_5	T_8	13	0.27	0.92	
G_5	T_9	13	−0.40	1.45	
G_5	T_m	13	0.29	1.00	
G_6	T_6	13	0.58	2.33	$0.02 < P < 0.05$
G_6	T_7	13	0.10	0.32	
G_6	T_8	13	0.35	1.23	
G_6	T_9	13	−0.40	1.46	
G_6	T_m	13	0.34	1.18	
G_7	T_6	13	0.47	1.79	
G_7	T_7	13	0.02	0.05	
G_7	T_8	13	0.32	1.11	
G_7	T_9	13	−0.50	1.93	
G_7	T_m	13	0.22	0.73	
G_8	T_6	13	0.38	1.36	
G_8	T_7	13	0.06	0.21	
G_8	T_8	13	0.45	1.65	
G_8	T_9	13	−0.23	0.80	
G_8	T_m	13	0.32	1.11	
G_9	T_6	7	0.27	0.61	
G_9	T_7	7	−0.01	0.02	
G_9	T_8	7	−0.02	0.05	
G_9	T_9	7	−0.49	1.25	
G_9	T_m	7	−0.076	0.17	
G_4	D	13	−0.45	1.66	$0.1 < P < 0.2$
G_5	D	13	−0.59	2.42	$0.02 < P < 0.05$
G_6	D	13	−0.61	2.53	$0.02 < P < 0.05$
G_7	D	13	−0.61	2.58	$0.02 < P < 0.05$
G_8	D	13	−0.44	1.61	$0.1 < P < 0.2$
G_9	D	7	−0.46	1.15	$0.2 < P < 0.4$

dalsvatn and include in the model the dependence of growth on temperature and population density. After having developed the model, we shall first see if it gives reasonably accurate yield estimates for past years. Thereafter the model shall be used to predict yields at varying mesh sizes at different levels of fishing effort.

A. *The model*

The basic model is the method described in section 10 C in RICKER (1958). Only trout that are four years or older are included.

The year is divided in the three periods:

June 1—July 31 when there is no fishing and half of the growth (G/2) takes place.

August 1—September 30 when all the fishing is done and a quarter of the growth (G/4) takes place.

October 1—May 31 when there is no fishing and a quarter of the growth takes place.

The natural mortality ($M=0.31$) is evenly distributed through the year with $M=0.05$ in each of the two first periods and $M=0.21$ in the last period.

The growth coefficients are computed from the equations:

$$G_4=0.1371+0.0746\cdot T_6—0.0015\cdot T_6\cdot D \tag{17}$$
$$G_5=0.082\ +0.0669\cdot T_6—0.0018\cdot T_6\cdot D \tag{18}$$
$$G_6=0.0901+0.0473\cdot T_6—0.0013\cdot T_6\cdot D \tag{19}$$
$$G_7=0.0944+0.0352\cdot T_6—0.0011\cdot T_6\cdot D \tag{20}$$
$$G_8=0.1596+0.0153\cdot T_6—0.0005\cdot T_6\cdot D \tag{21}$$

For trout that are 9 years or older we shall use $G=0.20$ independent of temperature and population density.

Our next need is to find equations to estimate the fishing mortalities that are caused on the exploited age groups by different mesh sizes at different levels of fishing effort:

Table 29. *Multiple linear regressions of G-values on June air temperature and population density 1958—70.*

Y	x_1	x_2	d.f.	a	$b_{y1.2}$	$b_{y2.1}$	R^2	$t_{y2.1}$	$t_{y1.2}$	$b'_{y1.2}$	$b'_{y2.1}$
G_4	T_6	D	10	0.3565	0.0568	−0.0192	0.641	3.50	2.55	0.66	−0.48
G_5	T_6	D	10	0.3335	0.0465	−0.0220	0.718	3.63	3.71	0.61	−0.62
G_6	T_6	D	10	0.2698	0.0323	−0.0157	0.739	3.77	3.96	0.61	−0.64
G_7	T_6	D	10	0.2454	0.0226	−0.0132	0.636	2.66	3.36	0.51	−0.64
G_8	T_6	D	10	0.2203	0.0101	−0.0053	0.354	1.59	1.80	0.40	−0.46
G_4	T_6	$T_6{\times}D$	10	0.1371	0.0746	−0.0015	0.643	4.16	2.57	0.87	−0.54
G_5	T_6	$T_6{\times}D$	10	0.0820	0.0669	−0.0018	0.724	4.76	3.77	0.88	−0.70
G_6	T_6	$T_6{\times}D$	10	0.0901	0.0473	−0.0013	0.768	5.29	4.35	0.89	−0.73
G_7	T_6	$T_6{\times}D$	10	0.0944	0.0352	−0.0011	0.665	3.91	3.63	0.79	−0.74
G_8	T_6	$T_6{\times}D$	10	0.1596	0.0153	−0.0005	0.384	2.24	1.97	0.62	−0.54

Table 30. *Original G-values (G) and values ($\hat{G}$) computed from formula (14).*

	1958		1959		1960		1961		1962		1963		1964		1965		1966		1967		1968		1969		1970	
	G	$\hat{G}$	G	$\hat{G}$	G	$\hat{G}$	G	$\hat{G}$	G	$\hat{G}$	G	$\hat{G}$	G	$\hat{G}$	G	$\hat{G}$	G	$\hat{G}$	G	$\hat{G}$	G	$\hat{G}$	G	$\hat{G}$	G	$\hat{G}$
G_4	0.66	0.66	0.69	0.76	0.80	0.84	0.90	0.85	0.63	0.77	1.00	1.03	0.97	0.79	0.80	0.82	0.90	0.99	0.75	0.82	1.03	0.93	1.00	1.03	1.02	0.98
G_5	0.46	0.45	0.53	0.54	0.61	0.62	0.68	0.66	0.52	0.61	0.84	0.83	0.73	0.62	0.62	0.64	0.77	0.78	0.58	0.65	0.88	0.74	0.73	0.82	0.76	0.73
G_6	0.37	0.34	0.40	0.41	0.45	0.47	0.50	0.49	0.39	0.46	0.65	0.61	0.55	0.46	0.45	0.48	0.56	0.58	0.44	0.49	0.61	0.56	0.58	0.61	0.53	0.54
G_7	0.29	0.25	0.29	0.30	0.34	0.35	0.35	0.37	0.32	0.36	0.53	0.47	0.45	0.36	0.32	0.37	0.41	0.44	0.33	0.38	0.46	0.43	0.44	0.46	0.40	0.40
G_8	0.25	0.22	0.26	0.25	0.28	0.27	0.28	0.28	0.24	0.27	0.38	0.32	0.32	0.27	0.27	0.28	0.25	0.31	0.25	0.28	0.34	0.30	0.32	0.32	0.29	0.29

Table 31. *Mean calculated lengths, fishing mortalities and selection values for different age groups of trout.*

Year	f	Age (years)																			
		4—5				5—6				6—7				7—8				8—9			
		$\bar{l}$	$\hat{F}$	$\hat{F}_{1000}$	Sel.	$\bar{l}$	$\hat{F}$	$\hat{F}_{1000}$	Sel.	$\bar{l}$	$\hat{F}$	$\hat{F}_{1000}$	Sel.	$\bar{l}$	$\hat{F}$	$\hat{F}_{1000}$	Sel.	$\bar{l}$	$\hat{F}$	$\hat{F}_{1000}$	Sel.
1960—61	1329	19.39	0.06	0.05	5.0	22.34	0.14	0.11	26.6	25.30	0.36	0.27	60.8	26.96	0.64	0.48	74.9	28.32	0.81	0.61	73.0
1961—62	1550	20.18	0.12	0.08	7.3	23.36	0.27	0.17	43.8	25.64	0.58	0.37	63.3	27.50	0.86	0.56	74.4	29.54	1.09	0.70	68.9
1962—63	1250	19.48	0.05	0.04	5.2	22.69	0.30	0.24	33.6	26.49	0.53	0.42	70.5	27.99	1.03	0.82	73.7	30.02	1.08	0.86	66.1
1965—66	1295	19.57	0.04	0.03	2.5	23.54	0.20	0.15	14.1	27.09	0.57	0.44	62.8	30.64	0.82	0.63	82.1	32.72	1.29	0.99	63.6
1966—67	1485	19.40	0.06	0.04	2.4	23.78	0.23	0.15	15.3	26.49	0.51	0.34	48.9	28.91	0.61	0.41	87.0	30.25	0.55	0.37	85.5
1967—68	1390	18.94	0.02	0.01	2.3	22.95	0.20	0.14	11.2	26.40	0.50	0.36	46.8	28.70	0.90	0.65	85.7	30.66	1.35	0.97	81.9

From estimates of survival rates and natural mortalities the fishing mortality can be estimated from:

$$\hat{F} = -\log_e \hat{S} - \widehat{M} \qquad (22)$$

The fact that the fishing mortality acted only during a part of the year does not bias this kind of estimate.

Estimated survival rates for the different age groups in different years were calculated from the figures in Table 21. These rates and $\widehat{M}=0.31$ were used in equation (22) to calculate the $\hat{F}$-values in Table 31.

Our next step is to correct the F estimates for variations in fishing effort from year to year. The yearly standard fishing efforts were listed in Table 1. We have by definition:

$$F = q \cdot f \qquad (23)$$

where q is the catchability coefficient and f the (standardised) fishing effort. As F is proportional with f we can easily correct our $\hat{F}$-figures to $\hat{F}_{1000}$ which is the estimated fishing mortality per 1000 gill-net nights with nylon nets. As seen in Table 31 there is a pronounced increase in $\hat{F}_{1000}$ with the age of the fish. This was expected as the youngest groups were too small for the meshes used and their catchability correspondingly low.

The calculated $\hat{F}_{1000}$-figures could be used in retrospect to check simple yield models, but they are useless for predicting trout yields when growth rates and mesh sizes are changed. We shall obviously need to relate trout *sizes* to $\hat{F}_{1000}$ and this is a difficult problem to solve from the available material.

In each of the years 1960—63 the same fleet of gill nets were used. Another fleet was used in the years 1965—68. We shall use these periods to construct the model.

We shall need estimates of the length distribution of the different year-classes in each year at the time when the fish were caught. As most of the catch was taken in the autumn, this will for trout of year-class i at age t approximately be the length distribution of year-class i when annulus (t+1) was laid down in the scales. Because of the gill-net selectivity the size distribution in the sample of trout of the year-class which were killed at age (t+1) will be biased. We shall instead use the back-calculated l_{t+1} for all fish of year-class i which were sampled at age l_{t+1} or older. The arithmetic means of these back-calculated lengths are listed as the $\bar{l}$-values in Table 31.

Let us consider the gill-net selectivity. Nylon gill nets with 30 mm mesh fish most efficiently on trout with length 30 mm · 9.4 = 282 mm which is the l_m for 30 mm nets (see Chapter III). The catchability on 30 mm nets for a group of trout which all have the length 282 mm is by definition the fraction of the group that is caught per unit of fishing effort with 30 mm nets. This catchability will be higher than for all other length groups, and for the different length groups the catchability must be proportional to the values of relative gill-net efficiency shown in Fig. 3. From equation (23) follows that F must be proportional to these values for relative gill-net efficiency.

However, our gill-net fleets contained nets with different mesh sizes. Obviously a fleet of 50 nets with different mesh sizes will be less efficient on 282 mm long fish than 50 nets that were all of 30 mm mesh size. For each net the efficiency for trout of modal length is 100, and the efficiency for trout of other lengths can be calculated from Fig. 3. For the 50 nets used in 1960—63 these efficiency values were added for each trout length and the sums divided by 50. These figures were used also for 1964. The same procedure was followed for the new combination of meshes used in later years. The figures obtained (Table 32) give the relative efficiency for the "average net" used in the different periods. These figures are comparable to single-mesh nets where the relative efficiency is 100 for fish of modal length.

Our next difficulty is that we are forced to use *mean* lengths for the different age groups in our model, but our values for gill-net efficiency were not estimated for mean lengths. This can give errors to our yield estimates, but we have to accept that. The selectivity figures in Table 31 were calculated from Table 32 by linear interpolation between cm-groups using $\bar{l}$ as length.

In Fig. 9 $\hat{F}_{1000}$ is plotted against the corresponding values for gill-net efficiency (from Table 31). Predictive linear regression of $\hat{F}_{1000}$ on gill-net efficiency gave the equation:

$$\hat{F}_{1000} = 0.011 + 0.007729 \cdot \text{Efficiency} \qquad (24)$$

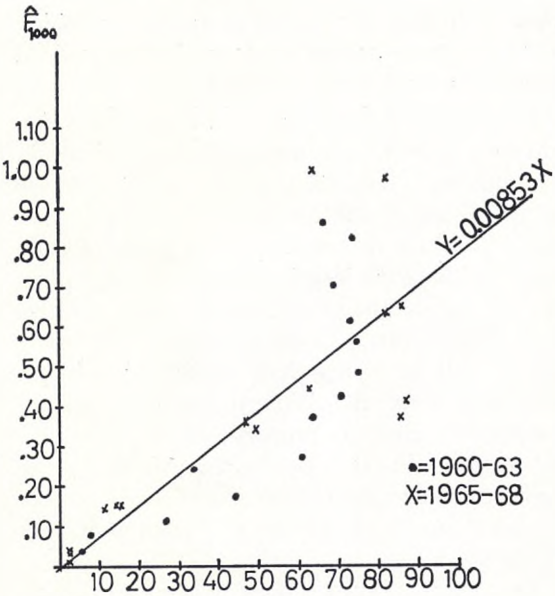

Fig. 9. Plot of $\hat{F}_{1000}$ against gill-net efficiency.

The slope of the regression line was significantly different from zero (t=7.38, d.f.=28). The correlation coefficient was r=0.81. However, as there were measuring errors in both variables and also heteroscedasticity, basic conditions for the significance tests have been violated. Probably the regression model 1 A (SNEDECOR 1956) is more appropriate. This gives the equation:

$$\hat{F}_{1000} = 0.00853 \cdot \text{Efficiency} \qquad (25)$$

For trout of modal length (efficiency=100) equation (24) predicts $\hat{F}_{1000}=0.78$ while equation (25) gives $\hat{F}_{1000}=0.85$.

The method used to relate F to gill-net efficiency is rough. One of the implicit conditions is that the nets shall never be placed so near each other that the catch on a net is influenced by the presence of neighbouring nets. The nets were usually bound together in links of 3—14 nets and placed approximately vertically on the shore line. Nets that are placed more or less parallel to the shore will usually catch less, and among fishermen the explanation is that the trout movements during the nights are mainly more or less parallel to the shore. A consequence of this is that nets in a link placed vertically on the shore line do probably not "shadow" each other. More important is probably the local, short-time depletion of catchable trout caused by the fishing. If a net or a link of nets is placed two or three nights in succession on the same spot, the catch will usually be best in the first night, be considerably reduced in the second night and be utterly reduced in the third night. If the nets are moved only 50—100 m away from the place where they were fishing the preceding night, this effect is avoided. Care was therefore taken to move the nets to new places every night (except in September 1966 as mentioned before) and usually there was more than 100 m between net-links. Due to this the "shadow-

Table 32. *Relative fishing efficiency for an "average net" of the net fleets used in different years.*

Period	Length (cm)																									
	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
1960—63	2.72	4.10	6.44	11.20	19.84	39.72	51.08	58.62	65.98	75.26	73.60	71.82	66.32	56.32	50.14	44.52	40.32	36.52	33.10	29.70	26.06	23.36	20.66	18.42	16.24	14.36
1965—68	2.12	2.30	2.64	3.98	7.36	11.36	16.42	24.38	37.44	60.90	81.50	87.56	87.72	78.90	72.80	60.06	54.50	49.26	44.02	39.48	35.58	31.98	29.02	26.30	22.88	21.18
1.8.71—30.6.72	27.63	34.25	35.75	30.25	25.63	22.00	21.63	24.13	24.50	22.75	22.25	22.00	23.88	25.63	27.63	29.25	31.25	30.88	30.38	30.38	32.25	31.50	31.00	30.63	29.50	29.25
1.7.72—	25.13	27.88	25.50	20.75	19.88	25.13	27.63	31.63	31.75	27.75	26.25	25.63	27.13	28.75	30.25	31.63	33.25	32.50	31.75	31.38	32.88	31.75	31.13	30.63	29.50	29.25

ing" effects between neighbouring net-links have probably been of minor consequence.

For conversion of the mean weight ($\bar{w}$) of an age group to mean length ($\bar{l}$) we need "year-class b's", but as we have seen, these vary from year to year. Trials showed that $b=3.17$ and $\log a = -5.38$ gave $\bar{l}$-values that were usually less than 5 per cent different from the $\bar{l}$-values listed in Table 31, and these values for b and log a were adopted to simplify the model.

B. Use of the model on the years 1960—68

We are now ready to check the model on the years 1960—68. Our starting point is a population density of $D=15.0$ kg per hectare on June 1 1960 (from Table 24) and the estimated numbers and total weights for the age groups that were listed in Tables 21 and 24. The procedure step by step for the year 1960 is shown in Table 33.

We start with 2387 four-year-old fish weighing 87100 g. This gives an average weight of 36.5 g.

With $T_6=13.5°C$ and $D=15.0$, G_4 is computed as:

$$G_4=0.1371+0.0746 \cdot 13.5-0.0015 \cdot 13.5 \cdot 15.0= \\ =0.84$$

This gives the G-values 0.42 for the period June 1 —July 31 and 0.21 for each of the periods August 1—September 30 and October 1—May 31. On October 1 the mean weight of the cohort will therefore be $36.5 \cdot e^{0.63}=68.5$ g. The corresponding mean length ($\bar{l}$) is computed from:

$$\log \bar{l}=\frac{\log 68.5+5.38}{3.17}=2.27624;\ \bar{l}=189 \text{ mm}$$

The gill-net efficiency factor for $l=189$ mm (called Eff. in the table) is taken from Table 32 by arithmetic interpolation and we obtain the value 3.96.

In 1960 the total fishing effort was 1329 gill-net nights, and we compute the fishing mortality as:

$$F=1.329 \cdot 0.00853 \cdot 3.96=0.04491$$

The average weight of the stock of four-year-old trout between August 1 and October 1 is 133824 g, and multiplied by F this gives a yield of 6.0 kg four-years fish in 1960. On June 1, 1961 the cohort is reduced to 1673 individuals weighing 141539 g, and these figures are used as the starting point for five-years fish in the computations for 1961.

The same procedure was followed for the other age groups in 1960, but the very few surviving 14-year-old fish were after 1 June each year excluded from the model as "dead from senility" to spare time on the computer. In the table there are small discrepancies between many of the tabulated values. The reason for this is that only two decimals are listed for F and G and one decimal for yield while the calculations on the computer were done with double precision arithmetic.

The total yield estimated for 1960 by the model is 611 kg while the actual yield in 1960 was 559 kg.

The model estimates the weight on 1 June 1961 for the age groups 5—14 years. To these figures were added the estimate of 125.6 kg four-year-old trout (from Table 24). The resulting biomass estimate was 911.6 kg and the corresponding population density 11.8 kg per hectare on June 1, 1961.

In this way we proceed from year to year after 1960; the number and total weight of the four-years recruitment are taken from Tables 21 and 24, while the number and biomass of the other age groups are provided by the model. The computed yields and population densities are shown in Table 34.

The greatest difference between observed and calculated yield occures in 1966 when the computed yield was 18 per cent too high. The total yield for the nine years as calculated by the model was only 2 kg smaller than the observed figure; but this very close fit is of course due to chance.

The number of fish that were caught in each year was computed from the equation

$$\text{Number caught}=\frac{N \cdot A \cdot F}{F+M}$$

where N is the computed number of a cohort surviving on 1 August, F and M the mortality coefficients for the period 1 August—1 October and A the corresponding rate of total mortality. Also for the total number of fish caught 1960—68 there is close agreement between the observed

Table 33. *Estimation of trout yield 1960 ($D=15.0$; $T_6=13.5$; $f=1.329$).*

Age	Date	N	$\overline{w}$	I	Eff.	F	G	M	G—F—M	e^{G-F-M}	Wt. stock	Av. wt. stock	Yield
4	1.6.60	2387	36.5								87100		
						0	0.42	0.05	0.37	1.4481			
4	1.8.60	2270									126125		
					3.96	0.04	0.21	0.05	0.12	1.1221		133824	6.0
4	1.10.60	2064	68.5	189							141524		
						0	0.21	0.21	0.00	1.0001			
5	1.6.61	1673									141539		
5	1.6.60	2775	67.5								187300		
						0	0.31	0.05	0.26	1.2974			
5	1.8.60	2639									242993		
					18.11	0.21	0.16	0.05	–0.10	0.9047		231413	47.5
5	1.10.60	2044	107.5	218							219833		
						0	0.16	0.21	–0.05	0.9466			
6	1.6.61	1657									208102		
6	1.6.60	2486	113.7								282700		
						0	0.23	0.05	0.18	1.2005			
6	1.8.60	2364									339368		
					56.36	0.64	0.12	0.05	–0.57	0.5641		265400	169.6
6	1.10.60	1187	161.2	247							191433		
						0	0.12	0.21	–0.09	0.9106			
7	1.6.61	962									174319		
7	1.6.60	1511	149.9								226500		
						0	0.17	0.05	0.12	1.1314			
7	1.8.60	1437									256254		
					68.78	0.78	0.09	0.05	–0.74	0.4758		189085	147.4
7	1.10.60	626	194.4	263							121917		
						0	0.09	0.21	–0.12	0.8840			
8	1.6.61	508									107775		
8	1.6.60	959	182.8								175300		
						0	0.13	0.05	0.08	1.0859			
8	1.8.60	912									190366		
					74.60	0.85	0.07	0.05	–0.83	0.4363		136711	115.6
8	1.10.60	372	223.0	274							83056		
						0	0.07	0.21	–0.14	0.8661			
9	1.6.61	301									71933		
9	1.6.60	496	212.5								105400		
						0	0.10	0.05	0.05	1.0513			
9	1.8.60	471									110803		
					73.07	0.83	0.05	0.05	–0.83	0.4368		79600	65.9
9	1.10.60	195	246.9	283							48397		
						0	0.05	0.21	–0.16	0.8521			
10	1.6.61	158									41241		
10	1.6.60	286	235.0								67200		
						0	0.10	0.05	0.05	1.0513			
10	1.8.60	272									70645		
					70.72	0.80	0.05	0.05	–0.80	0.4486		51166	41.0
10	1.10.60	116	273.0	292							31688		
						0	0.05	0.21	–0.16	0.8521			
11	1.6.61	94									27002		
11	1.6.60	108	269.4								29100		
						0	0.10	0.05	0.05	1.0513			
11	1.8.60	102									30591		
					61.32	0.70	0.05	0.05	–0.70	0.4990		22927	15.9
11	1.10.60	48	313.0	305							15264		
						0	0.05	0.21	–0.16	0.8521			
12	1.6.61	39									13007		

Table 33 (continued)

Age	Date	N	$\overline{w}$	$\overline{I}$	Eff.	F	G	M	G—F—M	e^{G-F-M}	Wt.stock	Av. wt. stock	Yield
12	1.6.60	7	300.0								2100		
						0	0.10	0.05	0.05	1.0513			
12	1.8.60	6									2207		
					52.61	0.60	0.05	0.05	−0.60	0.5508		1711	1.0
12	1.10.60	3	348.5	316							1215		
						0	0.05	0.21	−0.16	0.8521			
13	1.6.61	2									1035		
												Total	611.0

figure and the model, but in some years there are differences exceeding 20 percent. A closer examination shows that the catches of 4-year-olds are usually underestimated, and this leads to over-estimates of 5- and 6-year-old fish in the following years.

The population densities on 1 June are consistently higher than in the earlier estimates but the differences do never exceed 15—16 per cent, and (more important) they do apparently not increase with time.

Apparently the model gives a reasonably accurate description of how the yields and population densities in these years were influenced by changes in June temperature, fishing effort, mesh sizes and recruitment.

C. *Use of the model to estimate equilibrium yields*

We shall now use the model to predict equilibrium (sustainable) yields from our lake for different mesh sizes at different levels of fishing effort.

We shall not increase the effort to more than 2000 gill-net nights (all in August-September) as a higher yearly effort (25.8 gill-net nights per hectare) is hardly realistic and because of the dangers involved in extrapolations from our regressions.

As we have seen, the increased fishing mortality from 1958 reduced the number of spawners substantially, but apparently this did not cause any significant reduction in the recruitment of 4-year-old fish. We shall postulate that even a yearly fishing effort of 2000 gill-net nights will not significantly influence the recruitment. The estimated mean number and weight of 4-year-old fish on 1 June 1958—70 was 3539 and 38.2 g and we shall use these figures for the constant recruitment in the model. We shall also keep T_6 constant, on 12.8°C, which is the mean June temperature for the years 1958—70.

Generations' experience in management of Norwegian trout lakes is that if the total fishing effort and mesh size in a lake does not vary much, the yield will be about the same from year to year

Table 34. *Observed and computed trout yields and population densities 1960—68.*

	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	Total
Observed yield (kg)	559	561	375	403	456	384	445	415	350	—	3948
Computed yield (kg)	611	571	345	359	453	320	525	460	302	—	3946
Observed number of fish caught (4—14 years)	2876	2869	1880	2052	2247	1633	1860	1737	1425	—	18579
Computed number of fish caught (4—14 years)	3392	2931	1787	1855	2354	1369	2288	1755	1118	—	18849
Population density estimate on 1 June (kg/ha)	15.0	11.7	8.6	8.2	10.0	11.0	10.4	9.2	8.0	9.3	—
Population density computed from the model	—	11.8	8.8	8.9	11.5	11.2	11.9	10.7	8.9	9.5	—

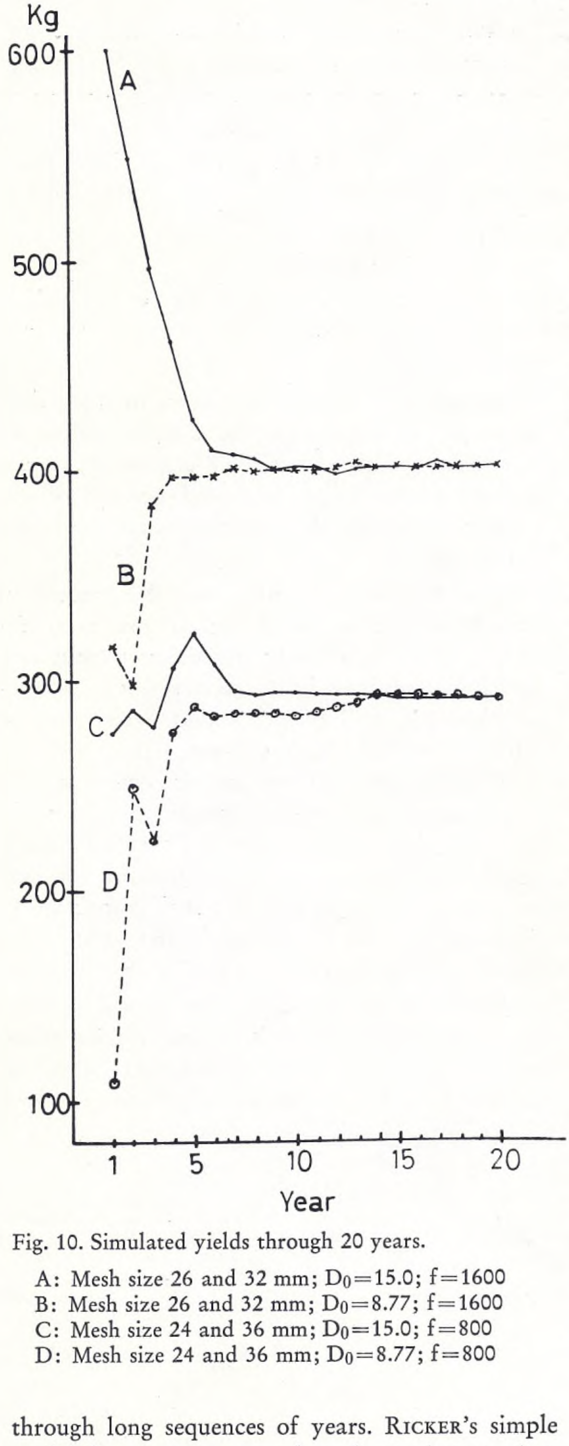

Fig. 10. Simulated yields through 20 years.

A: Mesh size 26 and 32 mm; $D_0=15.0$; $f=1600$
B: Mesh size 26 and 32 mm; $D_0=8.77$; $f=1600$
C: Mesh size 24 and 36 mm; $D_0=15.0$; $f=800$
D: Mesh size 24 and 36 mm; $D_0=8.77$; $f=800$

through long sequences of years. Ricker's simple model for constant growth and recruitment gives the same result, namely that if the fishing mortality within age is the same from year to year the predicted yield will, after a transitional period be stabilized to an "equilibrium yield". In our modification of the model, complex associations exist between fishing mortalities, growth rates and population densities, so let us check that the model still predicts equilibrium yields when the fishing efforts and mesh sizes are kept constant through a sequence of years. These equilibrium yields should be independent of the initial population density, and therefore trials were done with initial densities of 15.00, 13.23 and 8.77 kg/ha. Sequences of 25 years were run on the computer for two levels of fishing effort with the three initial population densities. With a fishing effort of 1600 net-nights per year, equally divided on mesh sizes 26 mm and 32 mm, an equilibrium yield of 402 kg was predicted after 9—10 years regardless of the initial population density. For an effort of only 800 net-nights, equally divided on 24 and 36 mm mesh, an equilibrium yield of 291 kg was predicted regardless of the initial population density. The results for the two extreme values of population density for 20 years are shown in Fig. 10.

Next, the model was used to predict the combination of mesh sizes and fishing efforts that would give the highest sustainable yield. Table 35 shows equilibrium yields for 98 combinations of mesh sizes and fishing efforts. Columns 2—8 show the yields for fishing with seven single mesh sizes from 24 to 51 mm, columns 9—14 show the results of combining equal numbers of nets of two sizes and in the last column the nets of the seven mesh sizes used in 1972—73 are combined. The highest sustainable yield is predicted for mesh size 32 mm.

The diminishing catch per effort for increased effort is clearly seen. For the 32 mm nets a sustained effort of 800 net-nights will in average give nearly 40 kg trout per 100 net-nights. An increase of the sustained effort to 1000 will give an average increase of only 20 kg per 100 net-nights. A sustained increase in effort from 1800 to 2000 net-nights will increase the catch with only 8 kg per 100 net-nights. Long before a sustained effort of 2000 net-nights is reached the economic value of the marginal catch has become too small to pay for an increase in effort, and probably this will happen before the fishing effort will be

Table 35. *Predicted equilibrium yields (kg) by different combinations of mesh size and fishing effort.*

Fishing effort	Mesh size													
	24	28	32	36	40	43, 5	51	24, 32	24, 40	24, 51	28, 36	28, 43.5	28, 51	24—51
800	262	311	318	243	157	102	43	295	262	195	306	260	227	251
1000	292	344	358	281	184	124	54	326	302	232	344	297	263	292
1200	316	369	390	318	206	144	65	353	331	264	373	328	296	324
1400	335	389	418	350	226	165	76	373	357	291	397	353	324	350
1600	351	404	443	380	244	185	86	387	378	313	417	373	345	371
1800	365	413	464	401	261	202	96	400	392	334	433	388	364	389
2000	375	419	480	423	276	215	107	410	403	348	443	404	379	405

sufficiently high to cause a decrease in the recruitment.

In many Norwegian mountain lakes yields of trout with mean weight exceeding 500 g have been obtained for a great many years. In Lake Ø. Heimdalsvatn the mean weight in the catches will be much smaller however the net-fishing is done (Table 36). Many Norwegian trout lakes are of this kind. The main reason is probably the large recruitment. We can probably reduce the recruitment to our lake to the magnitude we may wish by building thresholds that are impassable for trout in the outlet and in the inlet streams. Let us use the model to examine the effects of recruitment reduction on the sustainable yields:

Table 37 shows the predicted equilibrium yields for five levels of recruitment combined with four levels of fishing effort and seven mesh sizes. With a yearly recruitment of 3000 mesh 32 mm will still give the highest yield. If the recruitment is reduced to 2000 36 mm mesh will be best, and with a recruitment of only 1000 the highest sustained yield will be obtained on 40 mm nets. However we combine fishing effort and mesh size the sustained yield will be smaller than the 480 kg obtained by recruitment 3539, effort 2000 and 32 mm nets.

Table 38 shows the predicted sustainable yields in kg/ha, the average weight in the catches and the corresponding population densities for five levels of recruitment and four mesh sizes. The efforts is kept constant on 1600 net-nights per year. With a recruitment of only 1000 mesh 40 and 43.5 mm will give nearly the same yield, but the average trout size on 43.5 mm nets will be considerably higher Even with this low recruitment the yield will be reduced if we use 51 mm nets, but the mean size in the catch will increase to 642 g. For all four mesh sizes a sustained increase in the recruitment will reduce the mean size of the trout in the catches. If fishing was done only with 51 mm nets at the prevailing recruitment (3539) the population density would rise to about 21 kg/ha and the mean weight in

Table 36. *Predicted number, average weight and population density for equilibrium yields at different levels of sustained fishing effort.*

Fishing effort	32 mm nets			40 mm nets			51 mm nets		
	Number caught	Average weight	Pop. density	Number caught	Average weight	Pop. density	Number caught	Average weight	Pop. density
800	1129	282	15.9	460	342	20.6	233	184	21.9
1000	1271	282	14.8	556	332	20.0	291	186	21.7
1200	1398	279	13.8	635	324	19.5	345	188	21.4
1400	1524	275	12.8	709	319	19.0	397	191	21.2
1600	1645	269	11.7	780	313	18.5	450	191	21.0
1800	1733	268	11.0	846	308	18.1	501	192	20.8
2000	1789	268	10.5	907	304	17.6	552	194	20.5

Table 37. *Predicted equilibrium yields (kg) at different combinations of recruitment, mesh size and fishing effort.*

Fishing effort	Recruitment	Mesh size 24	28	32	36	40	43.5	51
800	1000	88	104	129	146	159	152	100
	1500	125	147	181	201	197	164	90
	2000	161	191	226	242	202	151	67
	2500	194	231	264	258	189	139	51
	3000	227	272	293	260	173	125	45
1200	1000	105	123	153	169	187	180	125
	1500	151	174	217	237	234	201	121
	2000	194	224	271	291	258	197	103
	2500	236	274	317	323	247	183	77
	3000	273	321	360	330	226	168	68
1600	1000	115	136	167	181	203	200	139
	1500	165	193	240	256	259	227	144
	2000	213	245	304	319	294	225	134
	2500	257	294	358	364	286	212	104
	3000	305	345	401	380	266	197	92
2000	1000	120	146	175	194	217	210	155
	1500	172	208	257	267	282	251	160
	2000	224	266	328	340	318	250	155
	2500	273	314	390	395	323	239	131
	3000	322	362	441	425	300	223	116

the catch would be reduced to about 190 g. At this high level of recruitment sustained fishing with smaller mesh would give higher mean weight in the catches.

Only by a substantial sustained reduction of the recruitment combined with the use of big mesh size can we increase the mean trout size in the catches to 600—700 g, but we cannot do this without reducing the yield substantially. If we want a sustained yield of 5 kg/ha or more from this lake we must accept a mean trout size of less than 300 g in the catches.

In 1958 after many years with very low fishing effort the population density was estimated to be 19.5 kg/ha (Table 24). The model predicts an equilibrium population density of 22.5 kg/ha if no fishing is done and the recruitment is fixed to 3953.

The model was also used to predict the influence on the sustained yield of a constant rise or fall in the mean June temperature. At a constant fishing effort of f=1600 and mesh size 32 mm the sustained yield would increase about 10 per cent from 443 kg to 482 kg if T_6 increased from

Table 38. *Predicted equilibrium yield, mean weight in catch and population density at differen levels of recruitment. f=1600.*

Recruitment	32 mm mesh Y_E (kg/ha)	$\overline{w}$	D	40 mm mesh Y_E (kg/ha)	$\overline{w}$	D	43.5 mm mesh Y_E (kg/ha)	$\overline{w}$	D	51 mm mesh Y_E (kg/ha)	$\overline{w}$	D
1000	2.15	346	4.6	2.62	529	5.5	2.58	605	6.5	1.79	642	8.9
1500	3.10	328	6.1	3.34	477	8.1	2.93	524	9.8	1.86	527	12.5
2000	3.92	311	7.5	3.79	446	10.7	2.90	454	12.9	1.73	415	15.3
2500	4.62	294	8.8	3.69	396	13.6	2.74	393	15.6	1.34	293	17.6
3539	5.72	269	11.7	3.15	313	18.5	2.39	303	19.9	1.11	191	21.0

12.8 to 13.8°C. A drop in T_6 to 11.8°C would decrease the sustained yield with about 10 per cent to 401 kg.

XI. DISCUSSION MANAGEMENT CONSIDERATIONS

No mathematic model can completely describe the complex web of events that result in trout yields, but only by using models can we hope with reasonable accuracy to predict changes in yield caused by management procedures. Our model is by necessity a crude, simplified approach, and we have violated some of the basic conditions for the statistical methods that have been used. For the selective action of gill nets we had to accept a rough unimodal curve, while the true curve is probably multimodal because trout can be entangled in gill nets in many more or less independent ways. We had also to accept the same constant natural mortality for all exploited age groups, but M varies probably both with age and with season and may be density-dependent also in the exploited cohorts. One of our rough tricks was to calculate the model's gill-net efficiency for each age group from the mean lengths of the age groups. The errors caused by this will be reduced when the net fleets are composed of many mesh sizes, but may well be important when the model is used to predict yields on a single mesh size. Besides, trout are individuals with individual behaviour and a capacity for learning, while we had to treat them as the lifeless white and black balls of the statistician.

In spite of these shortcomings, the model describes the yields in past years with reasonable accuracy and predicts the low yields and big trout sizes that are found in some of our mountain lakes with inadequate recruitment.

Data from the years 1957—71 have been used to develop the model. The model's yield output for these same years can therefore hardly be used to evalute the predictive accuracy of the model. The fishery research work in the lake continues, and the intention is to use the material from a sequence of years after 1971 for an independent check of the model. A new change in mesh size to 32 mm shall take place in 1976.

For the management of Ø. Heimdalsvatn the results of our study are important. Another question is to what extent they can be applied to other mountain lakes harbouring only trout. The same kind of model can probably be used, but with other constants. For instance we can probably in lakes of this kind describe the trout growth by equations of the general form

$$G_n = a_1 + a_2T — a_3T \cdot D$$

where T is a temperature variable and a_1, a_2 and a_3 parameters that will change from lake to lake. As the trout growth in our lake is positively correlated with the June temperature one could expect a negative correlation between trout yield potential and altitude. However, in lowland lakes the water temperature may during parts of the summer be above the optimum values for trout growth. Besides, the correlation between temperature and growth in our lake does not prove that the growth is directly influenced by the temperature — the influence can be secondary, for instance by inrceased food animal production or availability at higher temperatures. To estimate the parameters a_1—a_3 is a tedious task involving growth studies at different levels of population density. We do obviously need quicker methods to evaluate trout yield potentials.

If all fishing were prevented in Ø. Heimdalsvatn, the trout population density would increase until it reached a certain equilibrium level. Our model predicts this level to be about 22.5 kg/ha, and the trout density found at the beginning of our experiment tends to confirm this value. At this density the lake is "overpopulated" with small, slow-growing trout of inferior quality, and the lake's capacity to produce trout food is probably fully exploited. The (equilibrium) density of over-populated trout is therefore probably associated with the lake's potential for trout production and trout yield. In Dahl's (1917) experiments the over-populated density in two trout tarns near Bergen was 8.6—8.7 kg/ha, while his yearly yield through four years' heavy fishing was about 2.5 kg/ha. In the 25 ha Indre Rødlivann the over-populated trout had an initial density of 4.3 kg/ha and after the first year's thinning out, Dahl's yearly yield was about 1.5 kg/ha. However, this lake also had a population of char. The catches taken by DAHL were probably near the sustained yields that could be taken from these over-populated lakes. In DAHL's lakes and in Ø. Heimdalsvatn the potential trout yields were apparently 1/3—1/4 of the density of the over-populated trout stocks. As trout population densities can fairly easily be estimated by tagging—recapture and catch/effort observations this may show a way to obtain rough estimates of the potential yields of over-populated trout lakes.

Another simple method for "guesstimating" potential yields from biomass and natural mortality was suggested by GULLAND (1971). Given an unexploited stock his expected potential yields is:

$$Y_{max} = x \cdot M \cdot B_0 \qquad (27)$$

where x is a factor which according to GULLAND probably lies close to 0.5. As $M \cdot B_0$ approximates the yearly production $(M \cdot \overline{B})$ of an unexploited stock in equilibrium, the equation predicts that the potential yield is about half the production of the unexploited stock. In Ø. Heimdalsvatn with potential yield 450 kg, $M = 0.31$ and $B_0 = 1744$ kg, x will be about 0.8. One of the reasons for this higher x-value is probably that the density dependence of fish growth is not included in GULLAND's multi-species model.

In exploited lakes harbouring only trout in the equilibrium situation, a possible short-cut is to predict the yield potential from simultaneous estimates of growth rates and population density. Provided that the natural mortalities do not vary grossly between lakes ot this kind, high G-values at a high population density should indicate a high yield potential, while low G-values at a low density should indicate a poor potential. High G-values at low densities will mainly indicate low recruitment and/or high fishing mortality and not per se tell much about the yield potential.

In our lake high sustained yields require high fishing mortalities, and this is probably applicable to all trout lakes with excellent recruitment conditions. Detailed regulations of fishing gear or methods, size limits etc. are usually unnecessary in lakes of this kind, provided that the spawners are allowed to fulfil their function. Our model is based on fishing efforts fairly evenly distributed all over the lake. Efforts specially directed against the spawning fraction, for instance by closing the outlet by rows of nets during the spawning migration, can probably cause reduced recruitment and collapse of the fishery.

In lakes with trout in combination with char or other fish species, calculations of trout growth, mortalities and yields at varying levels of exploitation are complicated by the interactions between fish species. The simplest case is small lakes with only two species, for instance trout and char. Lakes of this kind are found in great number in Norway, and long-time studies of their population dynamics could be very rewarding.

XII SUMMARY

1) The fishery in Lake Øvre Heimdalsvatn has been completely controlled since 1958. Brown trout and a negligibly small population of minnows are the only fish species present. In 1957—58 the lake harboured a very dense trout population which was substantially reduced by heavy fishing in the following years.

2) The selectivity of gill nets was studied and an approximate, uni-modal selectivity curve for brown trout worked out. The combined selectivity for the fleets of nets used in the different years was calculated.

3) The movements of tagged trout were studied. Emigration from the lake was negligible. Individual trout showed a strong tendency to keep within some small part of the lake for very long periods.

4) Age and growth was back-calculated from scale impressions on celluloid. For trout lengths down to 15 cm eventual allometry between fish growth and scale growth was too small to be detected by the methods used.

5) LEE's phenomenon was clearly seen in the material. Errors in back-calculated lengths caused by selective sampling were found to be unimportant.

6) The length—weight relationship was studied. The "condition" factor increased significantly with trout length. The general formula $w = a \cdot l^b$ was used. In 1957—58 b was not significantly different from 3.0, in all later years b was significantly higher than 3.0. The reduction of trout biomass (density) induced an increase in b.

7) Coefficients for exponential growth rates, G, were calculated. The reduction of the population density led to a substantial increase in growth rates.

8) The increased fishing mortality caused a very pronounced decrease in the fraction of adult trout in the population. A part of this decrease was caused by the decreased mean age of the population, but there was also a pronounced decrease of the percentage adults in the age groups five, six and seven years.

9) Tag losses (Carlin tags) were negligible in the year of tagging and in the following year. Later on the tags were probably lost at an increasing rate.

10) The rates of survival in different years were estimated by means of two consequtive years' tagging and recapture. The results were checked by means of the biostatistical method (Ricker, 1971). As also the distribution of the fishing mortality of the tagged fish was known, a method described by Regier (1962) could be used to estimate M. $\widehat{M}$ varied in 1961—68 between 0.16 and 0.44 with geometric mean 0.31, and this last value was accepted as the best estimate of M. A constant monthly natural mortality of 0.31/12 was accepted.

11) A modification of Paloheimo's (1958) method was used to estimate the year-classes that had been fished to extinction. The results showed good agreements with Petersen estimates corrected for recruitment. In this way complete population estimates were obtained for the years 1958—66. For the years 1967—71 the estimates were completed with estimates based on catch/effort observations.

12) The biomass of trout elder than 3 years was estimated for the years 1958—70. The trout density (D) was 19.5 kg/ha in 1958, and the heavy fishing reduced it gradually to 8.2 kg/ha in 1963.

13) A significant negative correlation was found between the growth coefficients and the trout population density. A positive correlation was found between growth and mean June air temperature at a neighbouring meteorological station.

14) Ricker's yield model was extended to include the density and temperature dependence of trout growth. For each year the input was: The number and weight of the 4+ fish on 1 June (recruitment), the mean June air temperature, the combined selectivity for the gill-net fleets used and the fishing effort. The output was the yearly yield in number and weight for each age group.

The model was tried on the years 1960—68 and gave reasonably accurate results — the greatest difference between observed and computed yield was 18 per cent.

As a second check it was controlled that the model predicted a yield equilibrium when the input parameters were kept constant through a sequence of years.

Simulation runs on the computer with the temperature and the recruitment kept constant on the observed means, showed that for 98 combinations of mesh sizes and fishing efforts 32 mm nets would give the highest sustainable yield. With a yearly effort of 1600 gill-net nights (20.6 gill-net nights per hectare) the predicted sustained yield on 32 mm mesh was 5.7 kg/ha of trout with mean weight 269 g. Simulation of different levels of recruitment showed that at low levels of recruitment the mean size in the catch could be more than doubled, but the sustainable yield would decrease substantially. The combination big-sized trout and high sustained yield can not be obtained.

15) Some simple methods to obtain rough estimates of a trout lake's yield potential were discussed.

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Growth, Mortality and Migrations of the Anadromous Char, *Salvelinus alpinus*, L., in the Vardnes River, Troms, Northern Norway

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I. INTRODUCTION

MATHISEN and BERG (1968) estimated the instantaneous daily growth rates in summer and winter for the anadromus char of the Vardnes River. Their aim was to show the pronounced seasonal variation in growth for this fish and the material was pooled regardless of size or sex.

As more material is now available, we can separate the growth of the two sexes and also take in account the size dependence of the growth. We can also obtain some information about the survival and the migrations of this little known fish.

II. MATERIAL

The location of the small Vardnes River is shown in Fig. 1. The river harbours populations of anadromous brown trout, Arctic char and Atlantic salmon. The river and the traps for descending and ascending fish were described by MATHISEN and BERG (1968). The traps were again used in 1967—70 and all trapped ascending and descending fish examined. All previously tagged fish were recorded, and all untagged fish were tagged below the front of the dorsal fin with a numbered CARLIN tag. For each fish the total length in cm and the weight to the nearest 10 g was recorded. As the sex could only be ascertained from external examination, many char could not be sexed.

The number of char tagged when descending (labelled "Out") and when ascending (labelled "Up") are shown in Table 1. A total of 6165 individuals were tagged and some of these were afterwards controlled in the traps in up to eight different seasons. The efficiency of the traps varied much from day to day depending on water flow and other factors. The great variation in the table mainly reflects variations in trapping efficiency.

III. GROWTH

One way to estimate length growth in this material is to use the method of MANZER and TAYLOR (RICKER 1975). One of the conditions for this is that there is a linear association between l_{t+1} and l_t.

The predictive linear regression was computed for l_{t+1} on l_t where l_t was the observed total length of a char caught in the up-stream or the down-stream trap and l_{t+1} the observed length of the same fish when controlled in the same trap approximately one year later. The results are shown in the upper part of Table 2, where N is the number of observations, $\bar{l}_t$ and $\bar{l}_{t+1}$ mean lengths, b the slope of the predictive regression line, s_b the standard error of b, and r the correlation coefficient. Apparently the regression lines will give a fairly accurate description of how the growth depends on length and sex for individual fish. They are not true WALFORD lines (WALFORD 1946) as these are obtained by plotting mean length at age (t+1) against mean length at age t.

The sex could only be acertained after the secondary sexual characters had been developed. The group "Sex unknown" contains therefore mostly growth observations from small, juvenile fish which were never recaptured in the traps after they had attained maturity. The groups "Females" and "Males" contain growth observa-

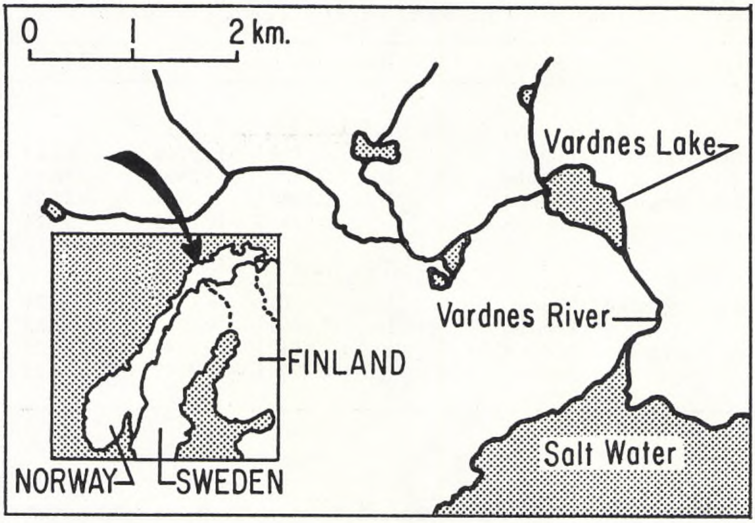

Fig. 1. Map of the Vardnes River (MATHISEN and BERG 1968).

Table 1. *Number of char tagged in the Vardnes River 1956—70.*

Year	Out	Up
1956	19	86
1957	34	8
1958	259	21
1959	223	170
1960	385	25
1961	267	78
1962	375	39
1963	66	47
1967	918	226
1968	770	114
1969	1122	17
1970	739	157
Total	5177	988

tions both from the juvenile and the mature periods of life.

The slopes of the regression lines for females, males and "Sex unknown" differ significantly. As young, fast-growing fish are over-represented in the last group, we shall leave it out in the further treatment of the growth data. Apparently the males grow faster than the females.

We have also some observations of char with two years between the control measurements, and the predictive linear regressions l_{t+2}/l_t for these fish are listed in the lower part of Table 2.

According to RICKER (1973, 1975) the geometric mean functional regressions can be preferable for bivariate distributions of this kind. The GM

Table 2. *Predictive linear regressions* l_{t+1}/l_t *and* l_{t+2}/l_t.

Sex	N	$\bar{l}_t$	$\bar{l}_{t+i}$	b	s_b	r
One year's growth						
Males	254	31.78	36.98	0.8198	0.0232	0.912
Females	254	32.61	36.96	0.7320	0.0237	0.889
Sex unknown	632	25.89	30.74	0.9566	0.0182	0.903
All fish	1140	28.70	33.51	0.8896	0.0110	0.923
Two years' growth						
Males	97	30.75	38.02	0.6270	0.0683	0.686
Females	95	30.94	37.92	0.5866	0.0550	0.742

Table 3. *Predictive and functional linear regressions of l_{t+i} on l_t. Estimated values of L_∞ and K.*

Regression type		Regression equation	L_∞	K
		One year's growth		
Predictive linear regression.	Males	$l_{t+1}=0.8198\,l_t+10.9268$	60.64	0.20
” ” ”	Females	$l_{t+1}=0.7320\,l_t+13.0895$	48.84	0.31
GM functional regression.	Males	$l_{t+1}=0.8989\,l_t+\ 8.4128$	83.21	0.11
” ” ”	Females	$l_{t+1}=0.8234\,l_t+10.1090$	57.24	0.19
		Two years' growth		
Predictive linear regression.	Males	$l_{t+2}=0.6270\,l_t+18.7398$	50.24	0.23
” ” ”	Females	$l_{t+2}=0.5866\,l_t+19.7706$	47.82	0.27
GM functional regression.	Males	$l_{t+2}=0.9140\,l_t+\ 9.9147$	115.29	0.05
” ” ”	Females	$l_{t+2}=0.7906\,l_t+13.4599$	64.28	0.12

regression lines pass through the means of all the observations $(\bar{l}_{t+i}, \bar{l}_t)$ with slope $v=\frac{b}{r}$.

The computed predictive and functional regression equations for the two sexes are shown in Table 3, and we have now to decide which set of equations gives the most reasonable results.

In VON BERTALANFFY's growth equation

$$l_t=L_\infty(1-e^{-K(t-t_0)})$$

which can be derived from the Walford line equation, the parameters L_∞ can be computed from the WALFORD line. HANCOCK (1965) who worked on cockles, used the same method on MANZER and TAYLOR lines and found values for L_∞ and K that were very similar to those obtained from the WALFORD lines. Let us assume that our regression lines can also be used to estimate the "asymptotic length" L_∞ and the curvature parameter K. L_∞ can then be estimated as the intersection between the regression line and the line $l_{t+1}=l_t$, and K can be estimated from the slope of the regression line which is e^{-Kt}. For the regression line for one year's growths $(l_{t+1}:l_t)$ the slope is e^{-K} and for lines describing two-years intervals $(l_{t+2}:l_t)$ the slope is e^{-2K}. The results are shown in Table 3. Apparently the L_∞ values calculated from the predictive regressions are more realistic than those from the GM regressions (the biggest fish in our sample of individuals were for females 59 cm and for males 60 cm). For the K-values the predictive regressions give the most consistent estimates.

Yearly increases in length can also be described by the simple exponential model $l_{t+1}=l_t \cdot e^G$ which can be written $G=\log_e(l_{t+1}/l_t)$. The common method is to estimate G between length means for the different ages. As the age is unknown in our samples, we shall compute individual G-values and average these within 5-cm groups. These calculated mean G-values for the two sexes are shown as points in Fig. 2. We can also estimate G-values from our regression equations by the formula

$$G=\log_e (b \cdot l_t+C)/l_t$$

where b is the slope and c the constant in the regression equation. This will give continuous curves showing estimated variation in G with length. These curves for the two sexes and the two types of linear regressions are also shown in Fig. 2. The curves based on the predictive regressions give the best fit to the estimated points.

IV. MORTALITY

The age of the char in our material is unknown, and we shall try to estimate survival rates from the tagging data. Table 4 shows for each year the number of char which were tagged when descending (Out) or ascending (Up). The fish were divided on five 10-cm groups. Within each of these groups are listed the number tagged (N), the number (Ctr.) that was later re-observed at least once at the weir and the number (R) that

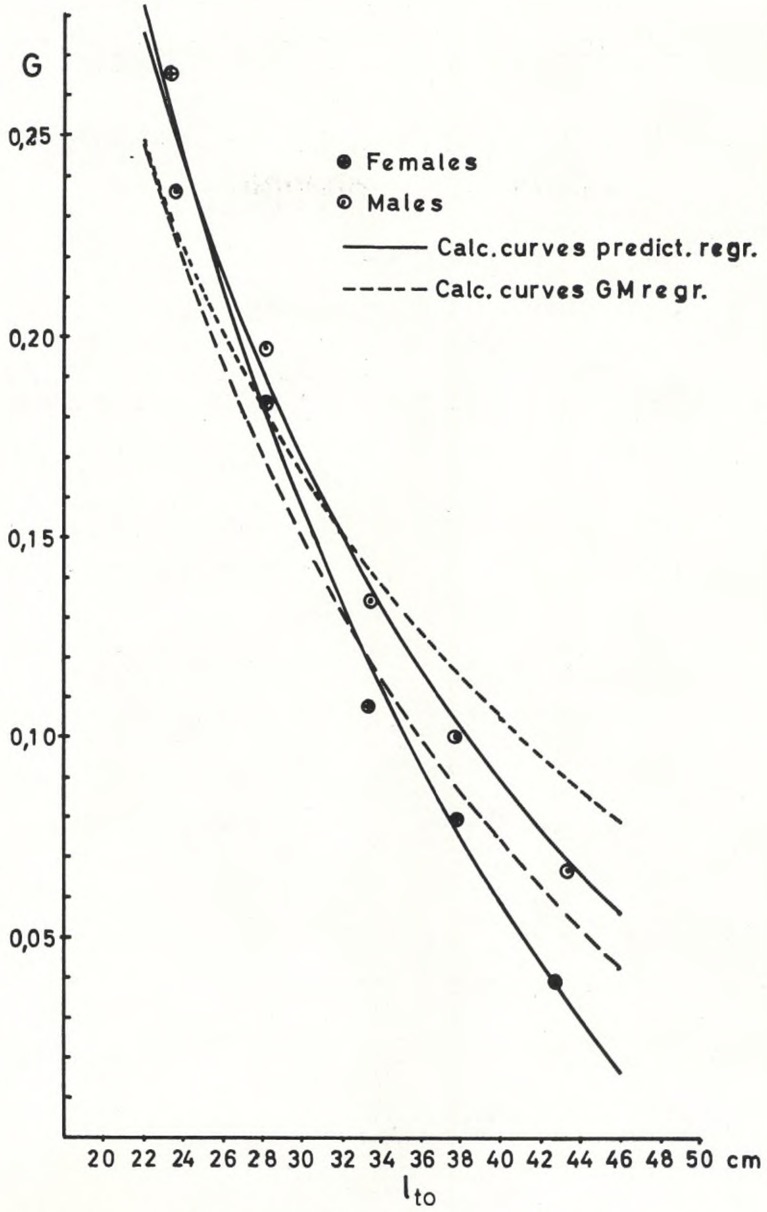

Fig. 2. Observed G-values (means within 5-cm groups) and G-curves calculated from predictive and GM regressions.

was reported caught by fishermen but had not previously been re-observed at their weir. Finally is for each group listed the percentage of tagged fish which was later either fished or re-observed at the weir and this is a minimum estimate of the survival percentage in the time period between descent and ascent (Out—Up) and between ascent and next year's descent (Up—Out). The main reasons why these survival estimates are too low are incomplete control at the weir, incomplete reporting of recaptures by fishermen, tagging mortality and tag losses. A further complication is

Table 4. *Minimum survival estimates of Vardnes River char. Explanations in the text.*

Group	≦ 20 cm				21—30 cm				31—40 cm				41—50 cm				51—60 cm				Total
	N	Ctr.	R	%	N	Ctr.	R	%	N	Ctr.	R	%	N	Ctr.	R	%	N	Ctr.	R	%	%
Out 1956	3	—	1	33.3	16	2	3	31.3	—	—	—	—	—	—	—	—	—	—	—	—	31.6
„ 1957	—	—	—	—	17	6	1	41.2	14	5	6	78.6	2	1	—	50	1	1	—	100	58.8
„ 1958	40	14	—	35.0	177	74	3	43.5	40	21	2	57.5	2	2	—	100	—	—	—	—	44.8
„ 1959	5	1	1	40.0	186	73	7	43.0	28	20	2	78.6	4	2	—	50	—	—	—	—	47.5
„ 1960	4	2	—	50.0	362	112	20	36.5	17	10	4	82.6	1	1	—	100	1	—	—	0	38.7
„ 1961	4	—	—	0	249	135	22	63.1	12	6	1	58.3	2	2	—	100	—	—	—	—	62.2
„ 1962	13	—	1	7.7	354	93	20	31.9	8	1	4	62.5	—	—	—	—	—	—	—	—	31.7
„ 1963	4	—	—	0	60	2	4	10.0	1	—	—	0	1	—	—	0	—	—	—	—	9.1
„ 1967	60	14	2	26.7	549	244	39	51.6	306	169	40	68.3	2	1	—	50	1	—	1	100	55.6
„ 1968	221	25	8	14.9	528	156	31	35.4	13	3	4	53.9	7	2	4	85.7	1	—	1	100	30.4
„ 1969	368	28	9	10.1	737	137	17	20.9	15	6	2	53.3	2	1	—	50	—	—	—	—	17.8
„ 1970	119	24	1	21.0	600	159	13	28.7	19	8	9	89.7	1	1	—	100	—	—	—	—	29.1
Total	841	108	23	15.58	3835	1193	180	35.80	473	249	74	68.29	24	13	4	70.83	4	1	2	75.00	35.68
Corr. total	837	108	22	15.53	3775	1191	176	36.21	472	249	74	68.43	23	13	4	73.91	4	1	2	75.00	36.00
Up 1956	—	—	—	—	62	14	21	56.5	24	1	9	41.7	—	—	—	—	—	—	—	—	52.3
„ 1957	—	—	—	—	7	6	—	85.7	—	—	—	—	1	1	—	100	—	—	—	—	87.5
„ 1958	—	—	—	—	—	—	—	—	15	10	1	73.3	6	4	1	83.3	—	—	—	—	76.2
„ 1959	—	—	—	—	159	113	11	78.0	11	8	—	72.7	—	—	—	—	—	—	—	—	77.7
„ 1960	—	—	—	—	10	6	1	70.0	10	10	—	100	4	3	—	75	1	—	—	0	80.0
„ 1961	—	—	—	—	57	40	6	80.7	20	10	2	60.0	1	1	—	100	—	—	—	—	75.6
„ 1962	—	—	—	—	18	1	5	33.3	21	2	7	42.9	—	—	—	—	—	—	—	—	38.5
„ 1963	—	—	—	—	42	—	8	19.1	5	—	1	20.0	—	—	—	—	—	—	—	—	19.2
„ 1967	—	—	—	—	32	14	3	53.1	82	43	13	68.3	111	73	13	77.5	1	—	—	0	70.4
„ 1968	2	—	—	0	102	76	2	76.5	9	7	1	88.9	1	—	—	0	—	—	—	—	75.4
„ 1969	1	1	—	100	8	3	—	37.5	7	4	—	57.1	1	—	—	0	—	—	—	—	47.1
„ 1970	3	—	—	0	118	—	8	6.8	30	—	2	6.7	6	—	1	16.7	—	—	—	—	7.0
Total	6	1	—	16.67	615	273	65	54.96	234	95	36	55.98	131	82	15	74.1	2	—	—	0	57.39
Corr. total	3	1	—	33.33	455	273	49	70.77	199	95	33	64.32	125	82	14	76.80	2	—	—	0	69.77

Table 5. *Estimated survival (minimum values) of 22 cm long descending char.*

Period	Males			Females			Yearly survival	
	I	G	S	I	G	S	$S_{Out-Out}$	S_{Up-Up}
Out year 0	22.0			22.0				
		0.275	0.36		0.282	0.36		
Up year 0	28.96			29.17			0.26	
		0	0.71		0	0.71		
Out year 1	28.96			29.17				0.26
		0.180	0.36		0.166	0.36		
Up year 1	34.68			34.43			0.23	
		0	0.64		0	0.64		
Out year 2	34.68			34.43				0.44
		0.126	0.68		0.102	0.68		
Up year 2	39.33			38.13			0.44	
		0	0.64		0	0.64		
Out year 3	39.33			38.13				0.44
		0.093	0.68		0.073	0.68		
Up year 3	43.17			41.02			0.52	
		0	0.77		0	0.77		
Out year 4	43.17			41.02				0.57
		0.070	0.74		0.051	0.74		
Up year 4	46.30			43.17			0.57	
		0	0.77		0	0.77		
Out year 5	46.30			43.17				0.57
		0.055	0.74		0.035	0.74		
Up year 5	48.91			44.70				

that a substantial number of River Vardnes char ascend other rivers.

The low rates estimated for 1963 and for Up 1970 are due to the traps being out of use in 1964—66 and after 1970. These periods were therefore excluded in the calculations of the mean rates that are listed at the bottom of the table. These means are our best minimum estimates of survival.

As we have treated both growth and survival as functions of length regardless of age, we can now combine the growth and survival estimates to construct tables of survival through sequences of years for cohorts with known lengths at first migration. In Table 5 we start with descending fish with length 22.0 cm. The corresponding growth coefficient, G, is 0.275 for the males and 0.282 for the females (taken from Fig. 2) while the rate of survival for both sexes in this first Out—Up period is 0.36 (from table 4). When ascending (Up year 0) the males have attained a mean length of 28.96 cm and the corresponding Up—Out survival rate for the next period is 0.71 The last columns in the table show the yearly survival rates based on the year between two descents (Out—Out) or two ascents (Up—Up). Again it should be emphasized that all survival figures in the table are minimum values for the survival of tagged char and they may grossly underestimate the true values for untagged fish.

Table 6 shows the reported recaptures by fishermen. R_1—R_7 are the numbers of recaptures in the first to the seventh year after the tagging. The yearly rates of exploitation were calculated from the recaptures the first year after tagging. For the descending fish these rates varied between 0.01 and 0.18 with a weighted mean of 0.04. For the ascending fish the rates of exploitation varied between 0 and 0.27 with a weighted mean of 0.11. The highly significant difference in recapture between the two groups is probably caused by a higher tagging mortality and a lower vulnerability to the fishing gear of the small descending fish.

The recaptures by the fishermen can also be used to estimate survival rates. For each group of tagged fish in Table 6 we should except the number of recaptures to be highest in the first year and then gradually to decrease because of mortality and tag losses. However, in many of

Table 6. *Recaptures by fishermen.*

Period of tagging		Number tagged	R_1	R_2	R_3	R_4	R_5	R_6	R_7	Total no. recaptured	Per cent recaptured
Up	1956	86	23	4	4	1	—	—	—	32	37
„	1957	8	—	1	2	1	—	—	—	4	50
„	1958	21	—	1	—	3	1	1	—	6	29
„	1959	170	10	13	17	3	2	1	—	46	27
„	1960	25	1	6	1	—	—	—	—	8	32
„	1961	78	14	10	2	—	—	—	—	26	33
„	1962	39	5	6	1	—	—	—	—	12	31
„	1963	47	3	4	2	—	—	—	—	9	19
„	1967	226	42	18	3	—	1	—	—	64	28
„	1968	114	6	8	4	4	—	—	—	22	19
„	1969	17	—	—	—	—	—	—	—	0	0
„	1970	157	5	5	1	—	—	—	—	11	7
Total		988	109	76	37	12	4	2	—	240	24.3
Out	1956	19	3	1	—	—	—	—	—	4	21
„	1957	34	6	1	2	—	—	—	—	9	26
„	1958	261	2	11	—	7	7	1	3	31	12
„	1959	223	13	3	1	13	2	—	—	32	14
„	1960	385	7	18	34	7	—	—	—	66	17
„	1961	267	10	25	13	4	—	—	—	52	19
„	1962	375	17	12	13	2	1	1	2	48	13
„	1963	66	2	—	—	—	1	1	—	4	6
„	1967	918	67	85	17	10	3	2	2	186	20
„	1968	770	37	17	10	2	4	—	—	70	9
„	1069	1122	20	12	6	7	1	—	—	46	4
„	1970	739	27	7	6	—	—	—	—	40	5
Total		5179	211	192	102	52	19	5	7	588	11.4

the groups the number of recaptures has been highest in the second and even in the third year, and this is especially the case for fish which were tagged when descending (labelled Out in the table). Many of these char are too small to be fully vulnerable to the fishing gear in use and we shall therefore leave out the first year's recaptures. There are also indications that the fishing mortality and/or the efficiency of reporting recaptures has varied considerably from year to year. For instance gave the groups Out 1959, 1960, 1961 and 1962 the highest number of recaptures in respectively year 4, 3, 2 and 1 after tagging. The reason was probably exceptionally good conditions for sea-fishing in the summer 1962. The same trend is present in the Up groups for 1958—61. Bias due to variations in fishing mortality and reporting efficiency among years can hardly be avoided in this material.

Our best estimates of yearly survivals are the fractions R_3/R_2. For the ascending char this gives

$S=37/76=0.49$

and for the descending char:

$S=102/192=0.53$

The difference between the two estimates is not significant.

The formula

$$S=\frac{R_3+R_4+\dots+R_n}{R_2+R_3+\dots+R_{n-1}}$$

gives slightly lower estimates, probably because of an increased rate of tag loss with time.

As the efficiency of the traps has varied very much from time to time, controls in the traps through successive years of cohorts of tagged fish can hardly be expected to give useful survival estimates.

Our conclusions are that among the exploited length groups the yearly survival is of a magnitude of 0.50. The mortality among the small, tagged fish is considerably higher, but this may at least partly, be an effect of handling and tagging. For vulnerable size groups the mean rate of exploita-

Table 7. *Vardnes River char. Migrations.*

	Distance from the Vardnes River											
	0	1—25 km	26—50 km	51—75 km	76—100 km	101—150 km	151—200 km	201—300 km	301—400 km	401—500 km	> 500 km	Total
No. recaptured freshwater	99	42	73	28	3	11	6	2	3	1	4	271
No. recaptured saltwater		412	82	29	11	12	4	3	1	2	—	556

tion was 0.11, but this is probably an underestimate because of incomplete reporting of recaptures.

V. MIGRATIONS

The timing of descent and ascent and the duration of the stay in the sea and in freshwater of the Vardnes River char was analysed by Mathisen and Berg (1968). In this paper we are mainly concerned with the migrations in the sea.

Table 7 shows the distance between the mouth of the Vardnes River and the points of recapture reported by fishermen. Most of the recaptures were made in the sea and most (74 %) of these within 25 km of the Vardnes River. 22 (4%)

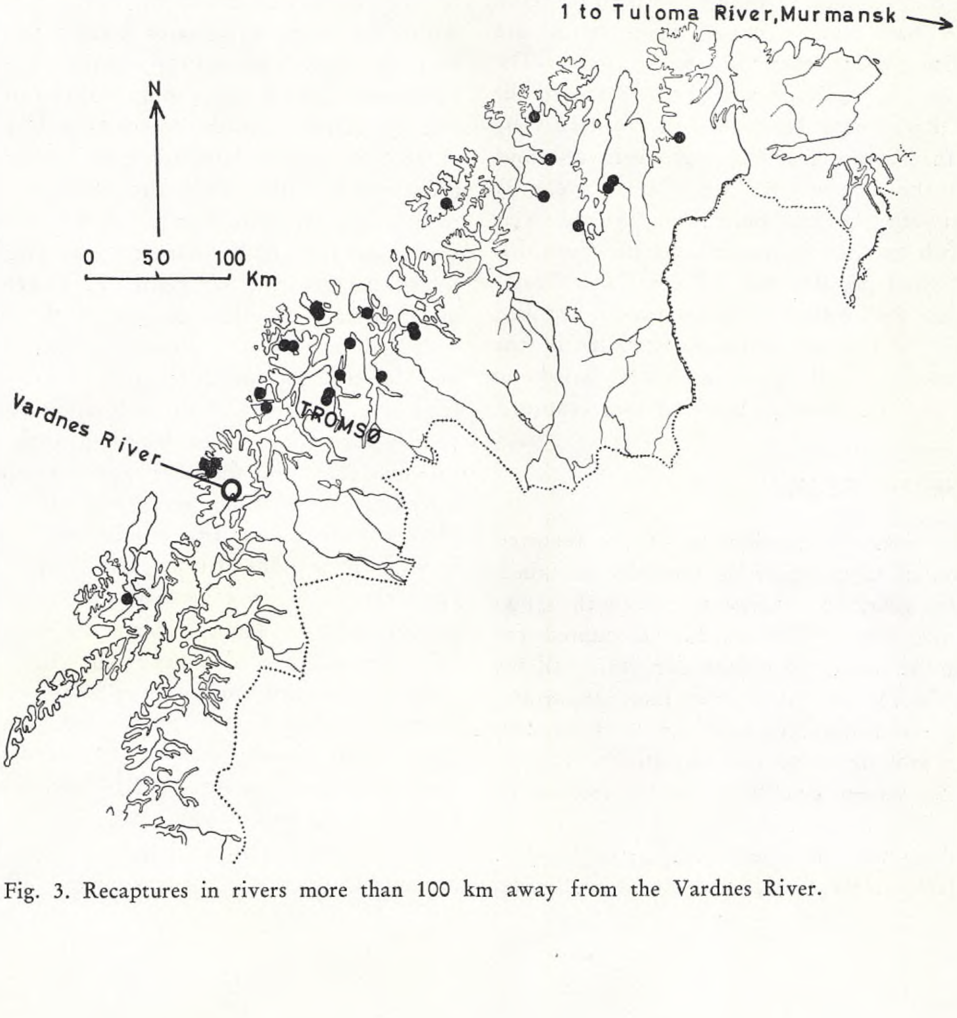

Fig. 3. Recaptures in rivers more than 100 km away from the Vardnes River.

Table 8. *Recaptures on different kinds of fishing gear.*

		Rod	Trolling	Gillnet	Bagnet	Seine	Total no.
Freshwater,	No.	225	2	38	—	—	265
,,	%	85	1	14	—	—	—
Saltwater,	No.	45	34	457	4	13	553
,,	%	8	6	83	1	2	—

of the sea recaptures were made more than 100 km away from the river mouth. Two of these fish were caught between 400 and 500 km away from the river.

Still more interesting are the 271 freshwater recaptures. Of these 99 were made in the Vardnes River and 173 in other rivers. 27 of these were made in rivers that were more than 100 km away, the localities are shown in Fig. 3. Of these 27 specimens 4 had been observed only once in the traps in the Vardnes River, 14 had been observed twice, 6 had been observed three times and three had been observed four times. The longest distance covered was the 940 km to the Tuloma River near Murmansk in the USSR by a char that before this had been registered four times in the Vardnes River. As there were 97 days between the last observation at the weir of this fish and the recapture date, the mean distance covered per day was 9.7 km. Next "best" was a char with estimated mean speed 6 km/day. These are of course, minimum estimates of the mean speed, as all speed estimates based on distance and time between marking and recapture.

VI. FISHING GEAR

Table 8 shows the distribution of the reported recaptures of tagged char on the different kinds of fishing gear. In freshwater rod with spoon or spinner, worm, fly etc. has accounted for 85 % of the catch and gillnets for nearly all the rest. In the sea the gillnets are most important, then come rods (usually near the river mouths) and then trolling, seine and bagnet. The bagnets are typical salmon gear with too big meshes for char.

As fishing was only permitted in the Vardnes Lake while the river itself was closed to fishing, the totals in the table can not be used for general reflections about the relative importance of sea- and freshwater fishing for anadromous char in the district.

VII. DISCUSSION

The lack of age determinations has made us regard growth as a function of length and independent of age. In species where the variance in length within the young age groups is great, this method may be advantageous. One question is how well MANZER—TAYLOR lines can be assumed to describe true population growth. As mentioned by RICKER (1958, 1975) these lines represent the growth of the surviving fish. They can therefore be used to compute the growth rates of the survivors of the tagged fish. As the handling and tagging may retard the growth, our computed G-values may underestimate the true growth of the surviving untagged part of the population. Further there may be considerable differences in growth rates from year to year. Very little is known about yearly variations in the length growth of anadromous char, and the small yearly samples have forced us to pool all years without weighting. However, the close fits of the regression lines may indicate that within fish lengths yearly variations in G have been of small consequense.

Very little is known about the natural and fishing mortalities of anadromous char. For the anadromous char from the River Salangselv, North Norway, NORDENG (1961) estimated from the age distribution a yearly survival rate of about 0.50 for mature fish. The rate of exploitation as calculated from tag returns was 0.36.

MOORE (1975) estimated the mean yearly natural mortality to 16 % between ages 10 and 20 years for the unexploited anadromous char from four rivers in the Cumberland Sound area of Baffin Island. The estimate was based on the age distribution of the pooled material from the four rivers.

For the Vardnes River char the data show an increase in survival rate with size. Although this could be expected, it may be an artifact caused by high mortality of small fish because of handling and tagging. For the exploited size groups our best survival estimate is of the magnitude $S=0.50$. As this estimate is based on fractions of the type R_3/R_2 one of the underlying assumptions is that the rate of reporting recaptures does not vary much from year to year.

A yearly survival of 0.50 is in good agreement with NORDENG's results. As we know that the reporting of recaptures is too low, we can not use the estimated rate of exploitation to separate fishing and natural mortalities without bias. Tentatively we can use MOORE's estimate of a yearly natural mortality of 16 % which corresponds to the instantaneous coefficient $M=0.17$. Combined with a survival rate of 0.50 this gives $F=0.52$ as a tentative estimate of the fishing mortality. Provided that the natural mortality is constant (monthly coefficient 0.17/12) the corresponding rate of exploitation will vary between 0.34 and 0.41, depending on the distribution through the year of the fishing mortality. This is again in good accordance with NORDENG's results. On the other hand our own rate of exploitation of 0.11 and survival of 0.50 would give a natural mortality of the magnitude $M=0.53$ which is probably a gross over-estimate.

The descent and ascent of anadromous char is easily observed and has been described by several authors. Especially the ascent has been of direct commercial interest as much of the char fishing in high latitudes is done in the river mouths when the fish return from the sea in late summer or early autumn.

The migrations in the sea, however, and eventual ascent in other rivers than the natural are little known as they have been studied in only some few places over the vast circumpolar distribution area of anadromous char.

Usually the char remain in a sea area fairly near to the river from which they descended, but HUNTER (1966) mentions that tagged char had been recaptured as far away as 80 miles from the river of origin. NORDENG (1968) found by tagging experiments in River Salangselv that the char kept to the neighbouring fjords within a maximum distance of 80—100 km from the river. GULLESTAD (1973) who tagged anadromous char on Spitzbergen mentions that his 60 reported recaptures were all made near the tagging sites. In the Cumberland Sound (Baffin Island) MOORE (1975) estimated from visual observations that the char were moving at a rate of 0.6—0.9 km/day away from the river mouths, and that the "average maximum" distance travelled from the natal river was 40—50 km. However, longer migrations by a fraction of the population and eventual ascents in other rivers than the natal would hardly be detected by the methods used by MOORE.

As we have seen, some of the char from the Vardnes River undertake much longer migrations than those mentioned above and with a speed that must be higher than suggested by MOORE.

The 99 recaptures by fishermen in the Vardnes River and the 173 recaptures in other rivers do, of course, reflect the fact that only a small amount of fishing was done in the Vardnes River. But still the 173 recaptures in other rivers indicate considerable straying, and as we have seen, not necessarily to neighbouring rivers. An important fact is that many of these fish, and especially the bigger specimens which had made the longest migrations already had been controlled two to four times in the Vardnes River.

There are apparently differences in the migration pattern from year to year, and especially the year 1968 was conspicious by the high number of recaptures in rivers more than 100 km away from the Vardnes River. Of the 27 recaptures of this kind 13 were made in 1968.

Comparisons with the results from the Vardnes River and River Salangselv (NORDENG 1968) which is only some 50 km away, indicate that even within the same district the migration pattern and the straying of anadromous char can vary considerably from river to river.

Evidently the migrations in the sea of anadromous char are not always as short nor as uniform as suggested in the sparse literature about the subject.

VIII. SUMMARY

A weir with traps for descending and ascending fish was constructed on the Vardnes River in 1956 and operated in 1956—63 and 1967—70. The river harbours populations of anadromous brown trout, Arctic char and Atlantic salmon. Only the char is considered in this paper.

The yearly length growth of the char was regarded as a function of initial length only. The instantaneous yearly growth rates were calculated from tagging data. The males were growing faster than the females.

The yearly rate of survival of the exploited part of the population was estimated to about 0.50. For the smallest length groups the survival rates were significantly lower, but this may partly be an effect of tagging mortality. The estimated rates of exploitation and natural mortality were probably grossly biased by incomplete reporting of recaptures by fishermen.

Most of the recaptures were done within 25 km of the mouth of the Vardnes River, but some specimens had travelled much farther. The longest recorded migrations was to a river 940 km away, and this distance was covered in 97 days. A considerable number of char entered other rivers and some of these fish had previously been controlled in up to four different seasons in the Vardnes River.

IX. ACKNOWLEDGMENTS

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A Method for Estimating Fish Length from Otolith Size[1]

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I. INTRODUCTION

Since ROLLEFSEN (1933) found that otoliths of old cod (*Gadus morhua* (L.)) often had more zones than corresponding scales, otoliths have often been used for age determination of marine fishes and sometimes for freshwater fishes (NORDENG 1961), especially Salmonidae. In spite of this, very few seem to have used otoliths for estimating fish growth in this family. To our knowledge, this has only been done for whitefish (*Coregonus lavaretus* (L.)) (AUSEN 1976), and Arctic char (*Salvelinus alpinus* (L.)) (DALENE 1973). Hitherto, scales have most commonly been used for estimating the length of fish during earlier stages in their life span (HILE 1970). The objectives of this paper are, for brown trout (*Salmo trutta* L.): (1) to choose the most appropriate otolith radius to be used for regression analysis (fish length on otolith radius), (2) to compare the goodness of fit for different regression models of fish length on otolith radius, (3) to study the validity of the assumptions underlying the application of regression analysis, and (4) to compare the use of otoliths versus scales for estimation of fish length. Earlier we (JONSSON and STENSETH 1976) have studied the applicability of different regression models of fish length on scale size for brown trout and found that the polynomials of higher order than two give the best fit. For all the regression models studied (Table 1) it was found that the residuals were not normally distributed, and that the variance of the residuals depended upon scale size and estimated fish length. It was therefore concluded that these models can only be used for estimating fish length, without giving confidence limits for the estimates. Except for large material, no tests of the regression models can be performed.

II. MATERIAL AND METHODS

The material consists of 1,729 fish from a landlocked population of brown trout collected from May 1972 to November 1973 in the Lake Lønavatn and the River Strandelvi, Western Norway (60°40'N; 6°28'E). The fish from the lake were caught mainly in beach seine and gill nets. In the river, at the inlet to the lake, specimens under 8 cm were caught with electrical fishing apparatus. Fish smaller than 10 cm were measured to the nearest 0.1 cm. Larger specimens were measured to the nearest 0.5 cm. This resulted in a maximal error of 2.5 per cent. The size distribution of fish caught is shown in Fig. 1.

One sacculus otolith from each fish was read under stereomicroscope (25×). (Zeiss immersion oil was used as a refraction medium. The refraction index was 1.515 at 20°C.) This image was then magnified by Zeiss Camera Lucida drawing apparatus 1.8 times and transferred to a strip of cardboard on which the scale edge was marked.

III. RESULTS

A. *The best otolith radius*

The number of hyaline zones (annuli) could most easily be determined along three radii, r_1, r_2, and r_3 (Fig. 2). To determine which of these radii gives the best correlation to fish length, the fishes (228) caught in July, 1972 were analysed. This material consisted of fish measuring from 9.5—32.0 cm (Fig. 1). Estimating the correlation coefficient between each of the three radii and the total fish length, we found the highest correlation between r_1 and the fish length. Using the test described by SNEDECOR and COCHRAN (1973; 185—188) these correlation coefficients differ significantly. Therefore we used the otolith radius r_1 in the further treatment. The error due to measurement of the otolith radius r_1 was estimated

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[1] Contribution from the Voss Project, Zoological Institute, University of Oslo.

Table 1. *The regression models (fish length on otolith radius) with estimated parameters for a land-locked population of brown trout (Salmo trutta L.) from Voss River System, Western Norway.*

The mean square deviations between estimated and observed fish length are given for the models shown, and for the equivalent models for fish length on scale radius.

Model number	Regressions of fish length on otolith radius with numerical parameters	Mean square deviation	
		Fish length on otolith radius	Fish length on scale radius[1]
1	$Y=-1.0+15.8\cdot X_0$	5.01	6.16
2	$Y=-2.0+17.5\cdot X_0-0.7\cdot X_0^2$	5.00	6.16
3	$Y=-8.2+34.7\cdot X_0-14.8\cdot X_0^2+3.6\cdot X_0^3$	4.68	5.67
4	$Y=2.6-8.4\cdot X_0+39.2\cdot X_0^2-23.1\cdot X_0^3+4.5\cdot X_0^4$	4.51	5.66
5	$\ln Y=\ln 14.9+1.1\cdot\ln X_0$	5.20	6.12
6	$\ln(Y+3.9)=\ln 18.2+0.86\cdot\ln X_0$	4.99	6.12

[1] Parameter values for the corresponding models are given in JONSSON and STENSETH (1976).

equal to 0.022 mm. This was done by measuring 27 otoliths of different size (representative of the total material) 40 independent times each. As the otolith radius r_1 varied between 0.22 and 3.0 mm in the material, the error due to measurement may be considered negligible. As a result the otolith radius may be treated as a non-random variable in the following regression analysis. Measuring r_1 of the two otoliths for any given fish from each side of 50 randomly chosen trouts, we found that these could differ by as much as 14 per cent. No systematic error was, however, found. Thus, the otolith used for further analysis was chosen at random.

B. *The best regression model*

The regression analysis is based on the models most commonly used for estimating fish length from scale size (HILE 1970; JONSSON and STENSETH 1976). These are given in Table 1.

We have used the mean square deviation between the observed, Y_u, and the predicted, $\hat{Y}_u$, fish length, i. e.

$$\mathrm{Dev}=\frac{1}{n}\sum_{u=1}^{n}(Y_u-\hat{Y}_u)^2 \qquad (1)$$

for comparing the goodness of fit to the data.

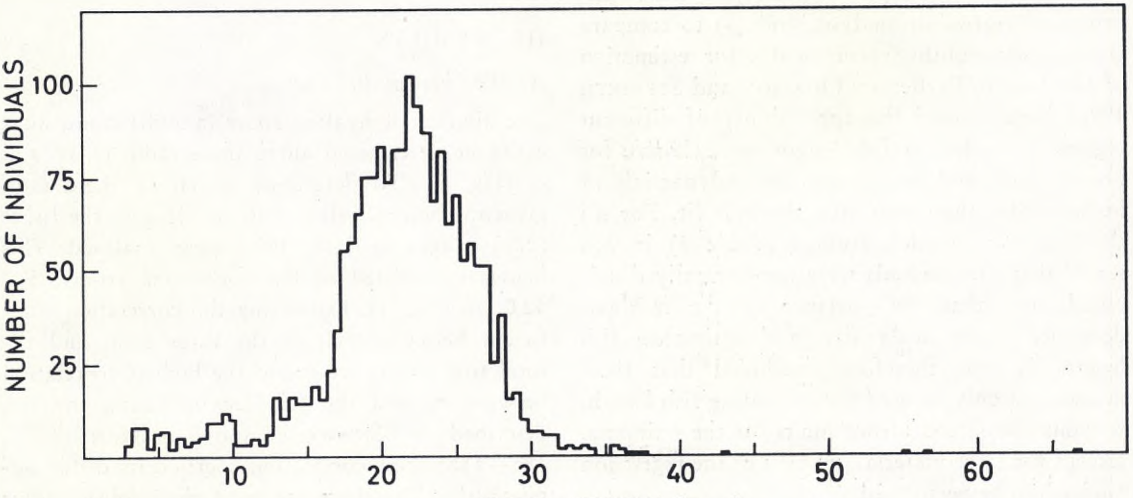

Fig. 1. Length distribution of the brown trout (*Salmo trutta* L.) from Lake Lønavatn, Western Norway.

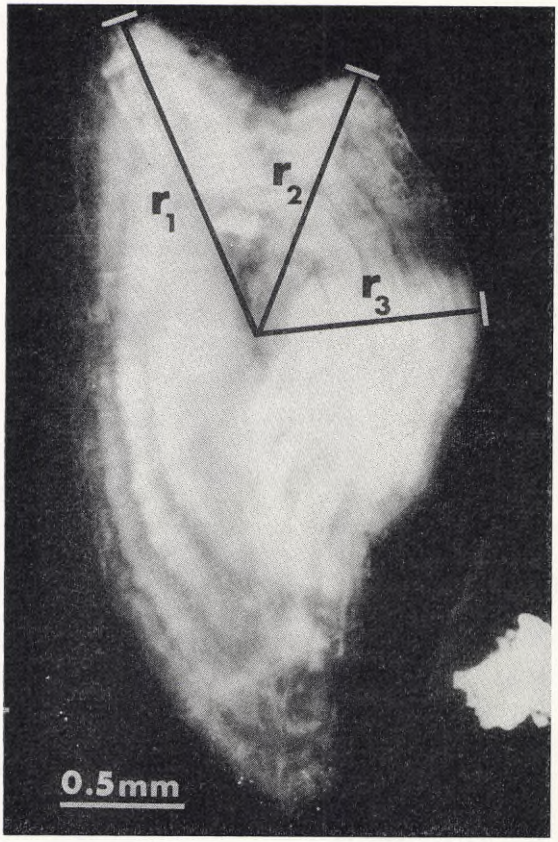

Fig. 2. Measured otolith radius of brown trout (*Salmo trutta* L.) from Lake Lønavatn, Western Norway.

The parameters in the model

$$\ln(Y-c) = a + b \cdot \ln X_0 \tag{2}$$

are found by the following technique: For a given value of c, the linear least square estimates for a and b are found. The c giving min (Dev) is then chosen (Fig. 3). Parameters in the models are found by linear least square techniques.

The least square estimates of the parameters in the regression models together with their mean square deviation between the observed and the predicted fish length (eq. (1)) are given in Table 1. Based on the mean square deviation the fourth degree polynomial is seen to give the best fit to the data. It is, however, pertinent to give a confidence interval which can only be given under the following assumptions: (1) that the residuals are normally distributed with expectancy equal to zero and constant variance, and (2) that these residuals are independent of each other, as well as the dependent and independent variables of the regression models.

C. *Evaluation of statistical assumptions*

In order to study the normality-property, we have employed KOLMOGOROV—SMIRNOV's test (GIBBONS 1971), and FISHER's g_1 and g_2 statistics (SOKAL and ROHLF 1969). The numerical values of these statistics are given in Table 2. The

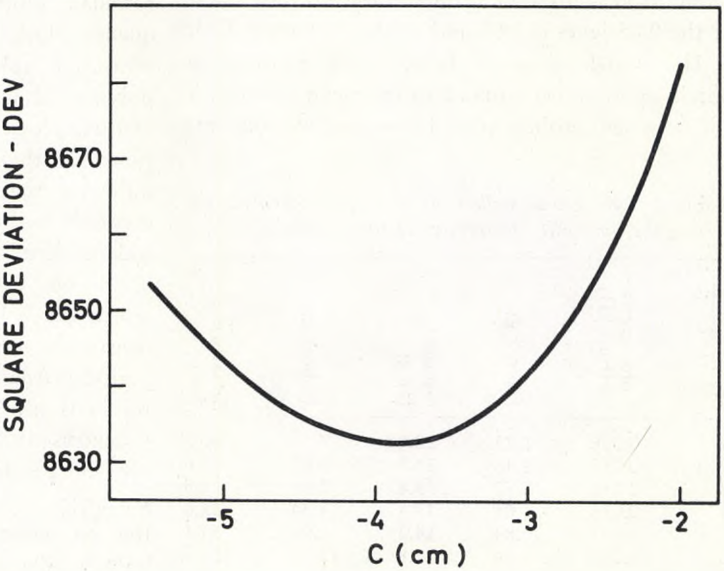

Fig. 3. The square deviation between the observed and the predicted fish length as a function of the parameter c in eq. (2). The other parameters in this model are the linear least square estimates for a given value of c.

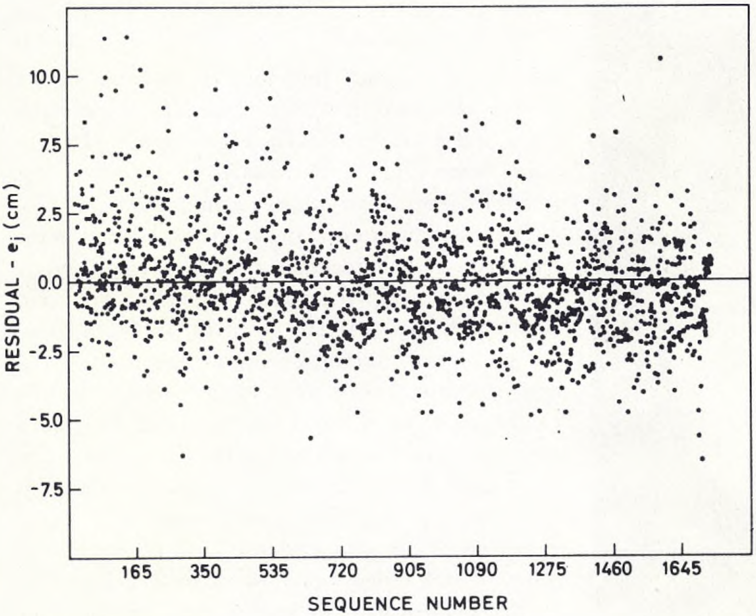

Fig. 4. Time sequence plot of the residuals for the fourth degree polynomial.

critical value for the KOLMOGOROV—SMIRNOV statistic (D) at the 0.05 level is 0.032 and at the 0.01 level 0.038. Consequently, we can conclude that the distribution of the residuals is different from the normal distribution. The numerical values of g_1 and g_2 show that the distribution of the residuals is skewed to the right, and is too sharp relative to normal distribution. Applying a t-test shows that both g_1 and g_2 are significantly different from zero. The critical value for the t-test at the 0.05 level is 1.65 and at the 0.01 level 2.33.

The models given in Table 1 may be used to obtain an unbiased estimate of the mean fish length for a given otolith size. However, without relying on the Central Limith Theorem (e.g. SNEDECOR and COCHRAN 1973) for large samples, we cannot give the confidence limits for these estimates. We can test neither the lack of the fit to the data using the F-test, nor whether the regression is significant or not.

Table 2. *Numerical values of the statistics used for testing the normality-properties of the residuals.*

Model number	Kolmogorov—Smirnov (D)	Fisher's g_1	T-statistic for g_1	Fisher's g_2	T-statistic for g_2
1	0.056	1.23	20.9	7.14	60.7
2	0.059	1.46	24.8	9.60	81.6
3	0.056	0.77	13.1	2.89	24.5
4	0.058	1.03	17.4	4.54	38.6
5	0.051	0.84	14.3	3.96	33.7
6	0.060	1.64	27.8	12.28	104.4

In order to study the constancy of the variance of the residuals we have made three different residual-plots (DRAPER and SMITH 1966): The residuals plotted against (1) time (i.e. time sequence plot), (2) estimated fish length, and (3) measured otolith size. The results for the fourth polynomial are given in Figs. 4—6 as an example of these plots. The general trends of the equivalent plots for the other models are the same. Fig. 4 indicates that the variance of the residuals is constant with respect to time, and that they are independent of each other. (As "time" is in a one-to-one correspondence with the sequence in which the fishes were analysed, these plots imply constancy in our method throughout the study period.) Analysing the sequence of signs of the residuals and applying the MANN—WITNEY U-test (GIBBONS 1971) also indicates that the residuals are independent. Figs. 5 and 6 show that the variance is not constant either with respect to the estimated fish length or to the measured otolith size. It might be possible to obtain a

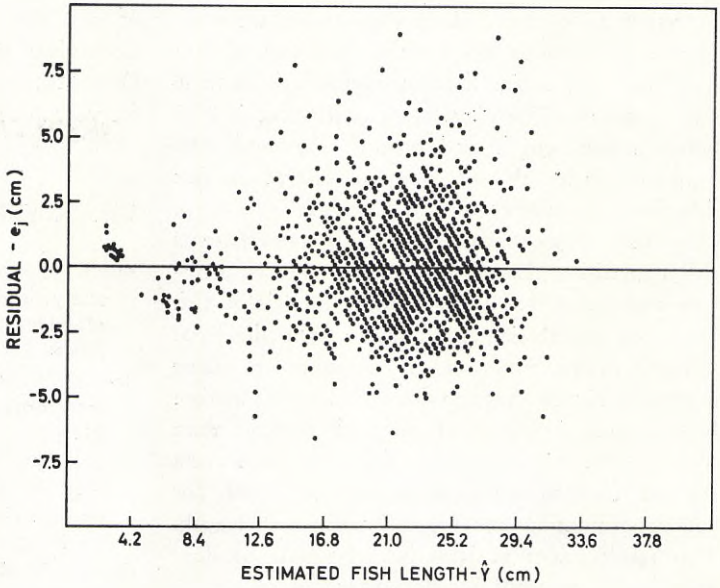

Fig. 5. Residuals plotted against the estimated fish length for the fourth degree polynomial.

constant variance and normal distribution of the residuals by including additional independent variables, applying weighted least squares, or by transformations (e.g. those proposed by Box and Cox (1964)). As the normality assumption is far from satisfied, we have not attempted to include such additional terms, nor have we applied any transformation of the observations.

IV. CONCLUSIONS

Based on this material we conclude that the assumptions underlying application of the regression analysis are not satisfied. It seems reasonable that this is a general result. We have found similar violations of these assumptions when scale size is used as the independent variable (Jonsson and

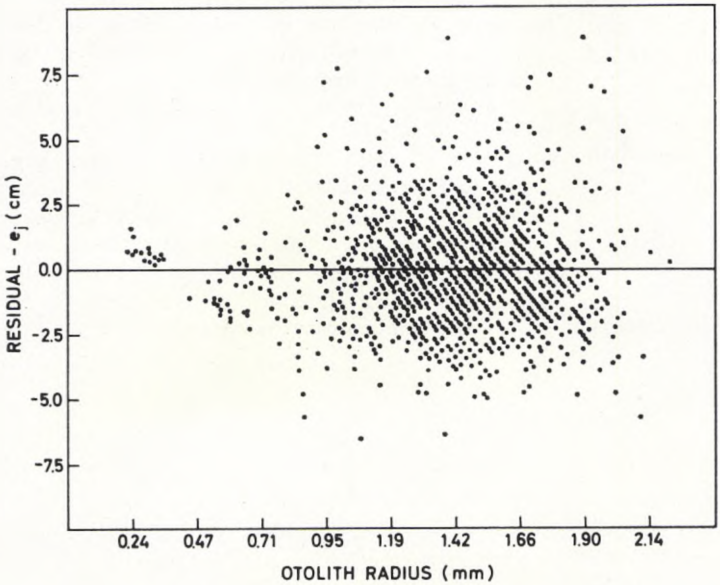

Fig. 6. Residuals plotted against the measured otolith size for the fourth degree polynomial.

Stenseth 1976). In all the models studied the mean square deviation is less for the regression of fish length on otolith size than for fish length on scale size (Table 1). The correlation coefficient is 0.92 between fish length and ototlith size and 0.88 between fish length and scale size. Use of the test described by Snedecor and Cochran (1973, p. 185—188) shows that these correlation coefficients differ significantly from each other. It is therefore concluded that the regression models of fish length on otolith size give a closer fit to the data.

Furthermore, Jonsson (1976) using the same material, showed that age determination of mature brown trout is more certain with otoliths than with scales. Consequently, for the population studied, otoliths are superior to scales both for age determination and for estimating fish length. This result might at least be applicable to slow growing brown trout populations in general.

V. SUMMARY

Based on otolith size, different regression models for estimating fish length have been analysed. Using land-locked brown trout (*Salmo trutta* L.) we have investigated the fit of different regression models. It is found that the fourth degree polynomial fits the data closer than the others. For all regression models it is found that the residuals are not normally distributed, and that the variance of the residuals depends upon the otolith size and the estimated fish length. Thus it is concluded that these models can be used for estimating fish length only. It is also concluded that the regression of fish length on the otolith size is better than that on the scale size.

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