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SWEDISH BOARD OF FISHERIES

INSTITUTE OF FRESHWATER RESEARCH

DROTTNINGHOLM

Report No 60

LUND 1982
BLOMS BOKTRYCKERI AB



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The Diet of Four Sympatric Whitefish Species in Lake Parkijaure

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ABSTRACT

Six basic whitefish populations are responsible for the present abundance of whitefish demes in Scandinavia. Four of them live sympatrically in Lake Parkijaure. Their vernacular names are large sparsely rakered whitefish ('storsik'), lesser sparsely rakered whitefish ('sandsik'), southern densely rakered whitefish ('planktonsik') and northern densely rakered whitefish ('aspsik').

Their number of gill rakers, growth rates and habitats were different and the sparsely rakered storsik and sandsik had a benthic diet, while the densely rakered planktonsik and aspsik were plankton feeders.

The benthic diet of storsik and sandsik was similar, but their size-biased predation was different. The smaller sizes of storsik fed on larger benthic prey than sandsik, while sandsik was flexible in diet and fed partly on plankton. The plankton diet of small sandsik was similar to the diet of planktonsik and aspsik, with the exclusion of calanoid copepods which were absent, suggesting that sandsik is a less skilled plankton hunter than the two planktophagous species. Aspsik performed vertical movements and shared the habitat of the benthic whitefish, although its diet was planktonic completed with surface food. The small planktonsik lived in midwater, feeding exclusively on zooplankton.

Five years after Lake Parkijaure was converted into a reservoir, positive effects of the damming-up phase such as better growth still obtained. The balance within the whitefish species group was as yet unaffected. The process of reduction of the benthic fauna had started, however, and the diet of the two benthic species was concentrated to few and smaller food items. Their feeding niches overlapped more than previously. The diet of the plankton feeders was not affected. The catches of all four species was lower.

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I. INTRODUCTION

The present investigation was originally intended as a study of the effects of water level fluctuation on the fish community in a lake, where test fishing was undertaken in midwater, both before and after the lake was transformed to a reservoir. During the investigation, it was discovered that Lake Parkijaure in the River Lilla Lule was inhabited by four well identified whitefish populations and another question arose, namely, what characterizes the interaction between different whitefish species.

The variety of forms of whitefish have caused the taxonomist great problems for many years and as a result, changes in the fish community have been difficult to interpret. SVÄRDSON (1979) discussed the speciation of Scandinavian *Coregonus* from an evolutionary point of view. He came to the conclusion that six basic whitefish populations are responsible for the present abundance of whitefish demes in Scandinavia. For practical purposes all six should be judged as separate species.

One important factor influencing the interaction between whitefish species is competition for food. Experiments have proved that diet preferences of different whitefish species have a considerable hereditary component (VOLOSHENKO 1973, SVÄRDSON 1979). Under natural conditions, however, feeding habits of the same species may vary from lake to lake, depending on, among several things, the lake habitat and species composition of the particular lake (LINDSTRÖM and NILSSON 1962).

On the other hand, within one lake, diets of closely related species, e.g. benthophagous whitefish, can overlap considerably (HOLMBERG 1975). Thus, the situation is complex. Whitefish sibling species can generally be split up into two main groups with regard to feeding habits, benthic feeders and plankton feeders. The diets between these groups are quite distinct (NILSSON 1958, 1960). The following paper will try to further identify the mechanism by which closely related whitefish species compete with one another.

Several aspects of whitefish reactions to water level fluctuations in connection with lake regulation have been described by LINDSTRÖM (1962, 1964, 1974). FÜRST, BOSTRÖM and HAMMAR (1980) have studied the fish community in a whitefish lake reservoir, after *Mysis relicta* was introduced.

II. METHODS

Lake Parkijaure is situated in the River Lilla Lule in Swedish Lapland at an altitude of 295 m, with a total area of 18 km² and a maximum depth of 40 metres (Fig. 1). The fish species of the lake are whitefish, perch, pike, trout, grayling and burbot. In order to cover the different habitats of the lake, a set of seven sinking gillnets, with mesh sizes knot to knot from 17 to 50 mm, were set at nine stations in the near shore zone. The midwater zone was fished at four depths from surface to bottom, with nine floating gillnets with mesh sizes from 10, 13, 17 to 50 mm.

The lake was fished during two seasons, two weeks in July and two weeks in September, just before impoundment in 1970 and five years after impoundment in 1975.

To identify the four species data from gill raker counts, growth histories and size at sexual maturity were combined. Historical notes on the fishing and information from local fishermen of local names and spawning habits of different whitefish forms were also taken into account. After the species were identified, catches from different depths and their feeding habits were analysed.

The near shore zone was relatively homogeneous, so samples from different littoral stations, although from the same depths, were pooled.

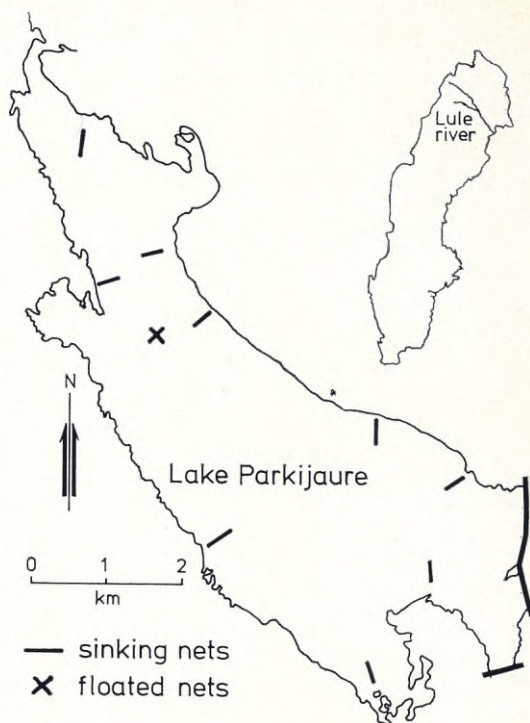


Fig. 1. Map of Parkijaure. The lake was fished with sinking gillnets at nine stations in the near shore zone and with floated nets from surface to bottom at one station in midwater.

Habitat differences between depths were considered to be of most interest. Thus, samples from depth zones e.g. 0–6, 6–12, 12–18 m were separated. The whitefish species were sorted into six size-classes viz. 10–15, 15–20, 20–30, 30–40 and 40–50 cm. From each size class, all stomachs within one depth zone were treated as a unit and a mean from each unit was calculated, using the per cent method. When the food composition by e.g. one size class of a species was to be analysed, a mean for that size class was calculated based on the means from all depth zones in proportion to the catch of each zone. In total, about 1,500 stomachs were analysed.

III. RESULTS

Gill rakers, growth and habitat

Data showed that there were four whitefish species in Parkijaure. The gill rakers varied in

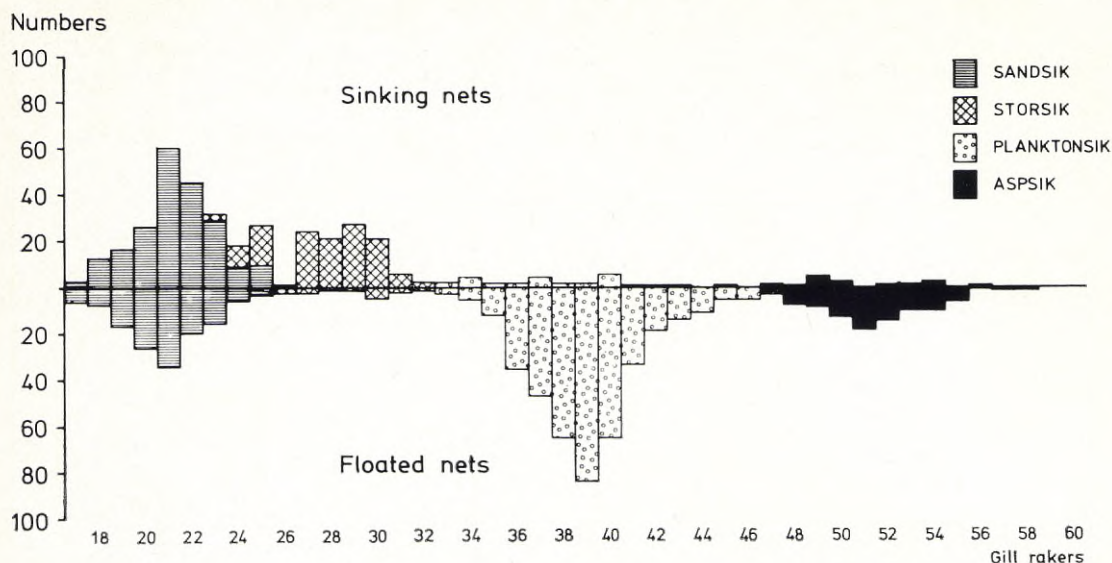


Fig. 2. Gill rakers of four whitefish species in Lake Parkijaure. Sandsik and storsik with few rakers were mainly caught in sinking nets. Planktonsik and aspsik with dense rakers were caught off shore in floated nets.

number from 16 to 58. Whitefish with few rakers were caught mainly in sinking nets while whitefish with many rakers in floated nets (Fig. 2). Following the nomenclature of SVÄRDSON (1979) the vernacular names in Swedish and English are

'Sandsik'	Lesser sparsely rakered whitefish
'Storsik'	Large sparsely rakered whitefish
'Planktonsik'	Southern densely rakered whitefish
'Aspsik'	Northern densely rakered whitefish

In the following, only the Swedish vernacular names will be used.

Sandsik had an average of 21 gill rakers and the mean was clearly separated from that of storsik, which had 27 gill rakers. Storsik had more rakers than in most other conspecific demes in Sweden and this is probably a result of introgression to aspsik. Aspsik had 50 rakers, which again indicates gene flow, since the least introgressed aspsik-deme of Lake Storvindeln has 60 (SVÄRDSON 1979). Planktonsik had an average of 39 rakers.

The four species had different growth rates.

Storsik and aspsik were large, sandsik and planktonsik were small (Fig. 3). The two small-sized species had a shorter lifespan than the large-sized species and they matured at around 14 cm, while the large species were sexually mature at around 25 cm.

According to information from local fishermen, storsik spawn along the shore in late December. Sandsik spawn earlier in November, often in running water. The spawning of aspsik is not well recorded in Parkijaure but in lakes nearby, aspsik is known to spawn in the main river in October. The spawning habits of planktonsik are not known.

The four species lived in different habitats, although the habitats overlapped. Storsik were caught in sinking nets in the near shore zone and were concentrated to depths less than 12 m. Sandsik had a broader spatial distribution and the concentration of catch was deeper than that of storsik. Sandsik were caught over the bottom in the littoral as well as in the profundal. Young sandsik were taken in floated nets in midwater. Planktonsik lived solely in midwater and dominated the catch in floated nets. Aspsik finally, were taken in the deepest part of the littoral zone and in floated nets over the bottom in the pro-

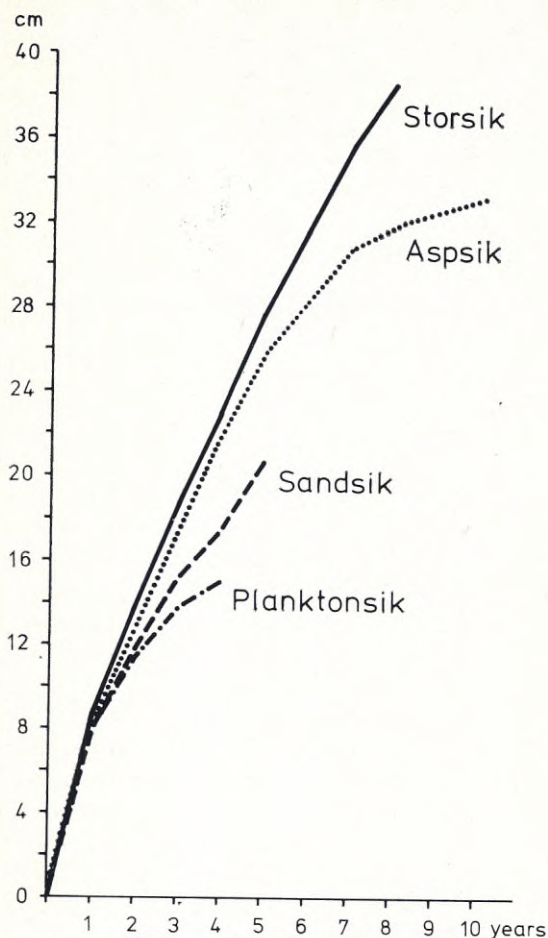


Fig. 3. The growth rates of sandsik, storsik, planktonsik and aspsik.

fundal. Aspsik also occurred, though sparsely, in midwater. The catches at different depths are given in Fig. 4.

Feeding habits

The species could be split up into two groups with regard to feeding habits. Storsik and sandsik were benthic feeders, planktonsik and aspsik were planktivorous.

The benthophagous pair, storsik and sandsik, fed on the same benthic prey, but the proportions of the various food items differed between the two species. The staple food of sandsik was chironomid larvae and small mussels of Sphaeriidae. Large insect larvae as those of Ephemero-

ptera and Trichoptera occurred in old fish. Storsik fed on chironomid larvae, snails of Valvatidae and insect larvae of Ephemeroptera and most of all Trichoptera.

The proportion of big insect larvae increased and dominated in the diet of large fish. For both species it was obvious, that the proportion of large benthic prey increased with the size of fish. However, there was a clear difference in the size-biased predation between storsik and sandsik. Comparing fish of the same size range, sandsik had eaten more chironomid larvae and small mussels, while storsik had taken a lot of large caddis larvae and snails (Fig. 5).

Benthic food dominated in the diet of the sparsely rakered species but zooplankton was also included. Small sandsik had eaten pelagically living *Bosmina coregoni* and *Daphnia cristata*. These were common in the diet of sandsik less than 15 cm, but the proportion decreased in larger fish. Consequently sandsik of 15–20 cm had a more pronounced benthic diet and this tendency was further stressed in sandsik larger than 20 cm. Storsik fed mainly on the semi-benthic *Eurycercus lamellatus*. Pelagically living zooplankton seldom occurred in its diet. Most storsik in the catch were larger than 15 cm and those had eaten *Eurycercus* regardless of size.

As seen in Fig. 5 storsik fed on insects captured at the surface. Like the number of gill rakers indicated gene flow this may reflect an introgression to aspsik as it is generally the aspsik which is associated with a diet of surface food.

The species composition of zooplankton in the diet changed with season and the proportion of plankton increased somewhat in September. In the same month, the proportion of empty stomachs was higher. The benthic food was similar in July and September, despite the changed species composition of chironomid larvae.

The diets of the two planktivorous species were based solely on pelagic zooplankton and were very similar. The food composition changed with season, but not with the size of fish. Many studies have shown that a correlation exists between the fish- and zooplankton faunas of a lake. The diet of planktonsik and aspsik was typical for a whitefish lake in northern Sweden, as found by NILSSON and PEJLER (1973). The most common food item

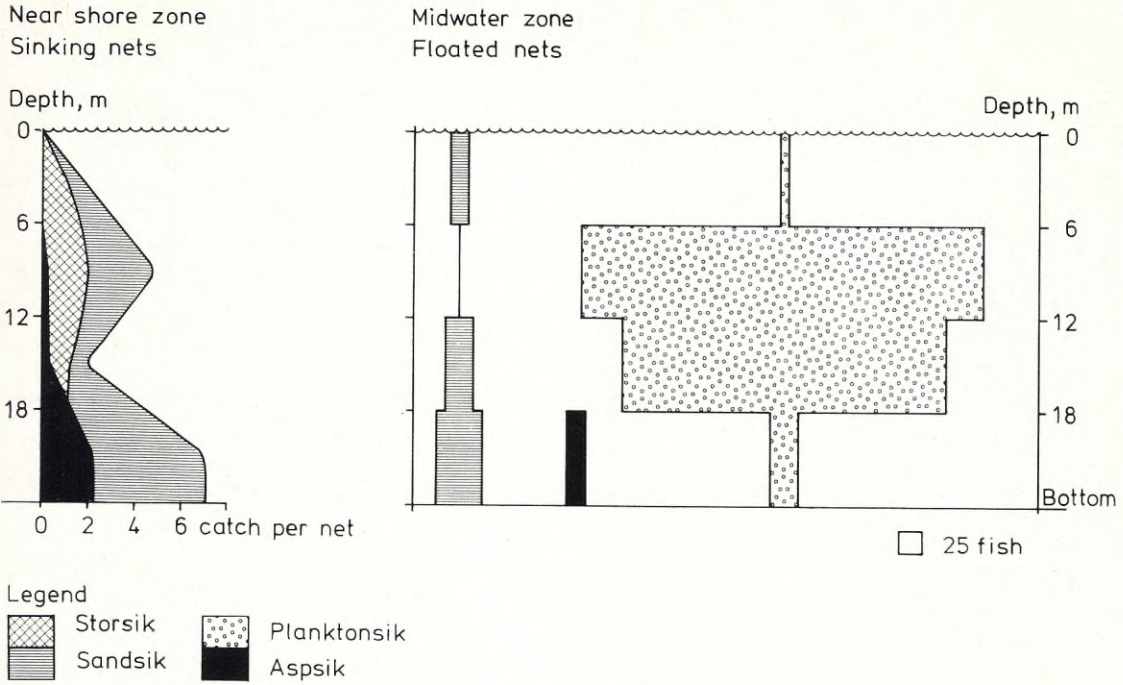


Fig. 4. The catch in sinking nets and floated nets. Storsik dwelt in the littoral zone. Sandsik had a broad spatial distribution and young sandsik were caught in midwater. Planktonsik lived in midwater, while aspsik were mainly caught in the profundal.

in July was *Bosmina coregoni*, *Heterocope saliens* and Cyclopidae spp, while *Daphnia cristata* dominated in the stomachs in September, followed by *Eudiaptomus graciloides*. The food content is given in Fig. 6 and Table 1. The diet of planktonsik was exclusively zooplankton, while aspsik fed on terrestrial insects from the surface as well. The proportion of empty stomachs was rather high for aspsik.

The planktonic food was composed of cladocerans as well as calanoid and cyclopoid copepods. A frequent conclusion is that cladocerans are more vulnerable than copepods, because copepods tend to escape by "jumping out of view" (NILSSON 1978). A specialized plankton feeder should therefore be skilful in capturing copepods. In this respect there was a clear difference in the plankton diet of the planktivorous species and sandsik, as the sandsik had eaten mainly cladocerans, a small quantity of cyclops but no calanoid copepods (Table 1).

Effects of lake regulation

In the first years after impoundment of a lake, during the damming-up phase, there are improved feeding conditions for the fish and most species benefit from this new situation. Some species may increase in number, affecting the interspecific relationship in the fish community, others will achieve a better growth, while their number remains unaffected. The whitefish in Parkijaure reacted with an improved growth (Fig. 7). The catch, however, was lower than before, while the number of pike and perch had improved (Table 2). It is well known that pike often increase when the shores are flooded. An occasional increase of the pike during the damming-up phase might have negatively influenced the whitefish population. Whatever the reason, however, assuming that the low catch of whitefish corresponded to a real decrease of the population, this, in combination with improved feeding conditions, could easily explain their good growth.

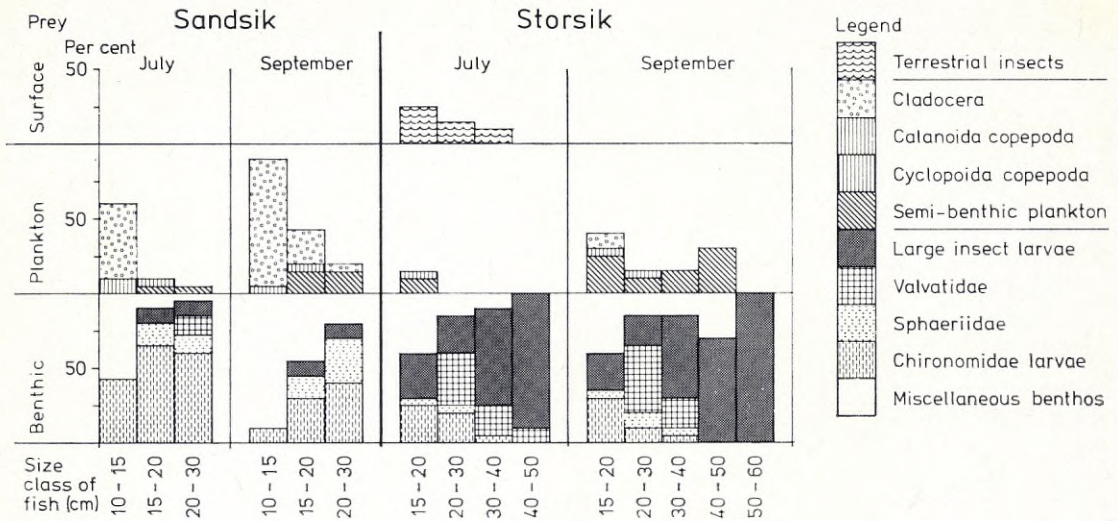


Figure 5.

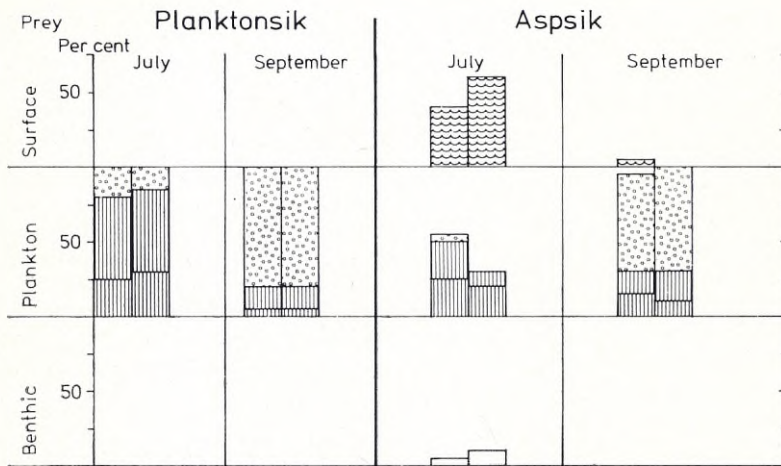


Figure 6.

Fig. 5. The diets of sandsik and storsik. Sandsik's staple food was chironomid larvae, while the main food of storsik was caddis larvae. This difference in diet was obvious also for fish of the same size range.

Fig. 6. The diets of planktonsik and aspsik. The diet of planktonsik was almost exclusively zooplankton, while aspsik fed on terrestrial insects as well.

While the catch of all whitefish species was low, the actual proportions of the different species remained unchanged and the habitats were the same as before (Table 3). So the balance within the whitefish species group was still stable.

The age-distribution, however, indicated some variation in the reactions of the species. In the sample of storsik 1975 there was a reduction of recruits (Table 4). Storsik is the most littoral species of the four and the spawning grounds

along the shore may have been affected by the subsidence of the water level in winter. It could also be, that an increase in pike had the greatest influence on storsik. The other species, especially the small-sized sandsik and planktonsik had more young fish in the 1975 sample.

Dynamic changes occur in a lake after impoundment and, in the long run, the reduction of the littoral benthic fauna is severest for the fish population. This process had already started in

Table 1. The zooplankton composition in per cent in the diets of small benthic sandsik and the planktivorous species pair planktonsik and aspsik.

Season	July			September		
	Sandsik 10—15 cm	Planktonsik 10—15 cm	Aspsik 20—30 cm	Sandsik 10—15 cm	Planktonsik 10—15 cm	Aspsik 20—30 cm
Zooplankton total	57	98	54	88	99	94
<i>Holopedium gibberum</i>	3	3	—	3	2	2
<i>Daphnia cristata</i> sens. str.	—	—	1	68	68	51
<i>Bosmina coregoni</i>	45	15	6	13	9	11
<i>Heterocope</i> spp.	—	54	23	—	—	—
<i>Eudiaptomus graciloides</i>	—	—	—	—	14	15
Cyclopidae spp.	9	26	24	4	6	15
Benthic prey	40	—	5	12	—	—
Surface prey	3	—	37	—	—	5
Miscellaneous food items	—	2	4	—	1	1
	100	100	100	100	100	100

Parkijaure, as seen from the diets of the benthic whitefish. The proportion of chironomids in the stomachs of storsik and sandsik had increased and the food was concentrated to just a few species. Even large storsik fed on chironomids. Large larvae of Mayflies and caddisflies had decreased in the storsik diet and were absent in sandsik. The earlier important caddis larva *Molanna angustata* was replaced by other species. So the diet of the two benthic species now overlapped considerably (Fig. 8). This is in marked contrast to the interactive segregation in trout and arctic char, in similar situation, as described in several papers by NILSSON (1960, 1963) and by NILSSON and PEJLER (1973). It seems that closely related species with similar feeding niches, react in other ways than more differentiated species, which increase their segregation into different feeding niches, as their com-

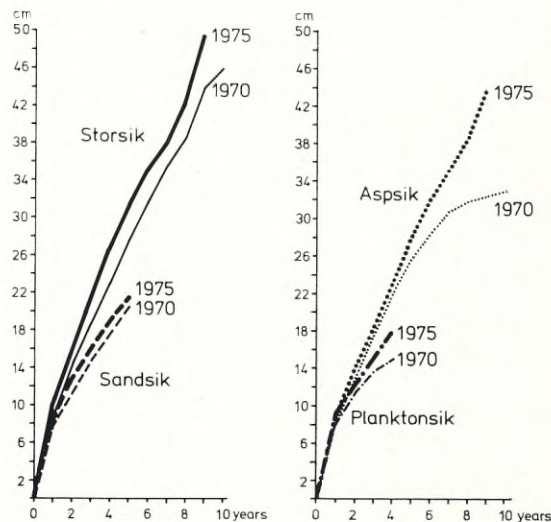


Fig. 7. Five years after impoundment of the lake, in 1975, the growth rates of all four species were improved.

Table 2. Catch of test-fishing (kg) before impoundment in 1970 and after impoundment in 1975.

		Whitefish		Perch		Pike		Burbot		Grayling		Trout	
		n	w	n	w	n	w	n	w	n	w	n	w
Sinking nets	1970	320	28	277	47	14	10	9	3	3	0.5	2	1
	1975	200	40	321	41	25	19	3	1	1	0.2	4	3
Floated nets	1970	3,896	91	5	1	1	2	13	5	0	0	0	0
	1975	2,750	48	11	1	0	0	2	0.4	0	0	0	0

Table 3. *The species composition of whitefish catch in numbers and per cent in July 1970 and in July 1975.*

		Storsik		Sandsik		Planktonsik		Aspsik	
		n	%	n	%	n	%	n	%
Sinking nets	1970	95	23	277	69	3	2	25	6
	1975	42	24	128	69	4	1	12	6
Floated nets	1970	2	0	170	12	705	79	70	8
	1975	1	0	67	16	319	76	31	7

mon resource, the bottom fauna, becomes gradually sparser.

Earlier studies have shown that the semi-benthic *Eurycercus lamellatus* is favoured during the first years after lake regulation (LINDSTRÖM 1973). The proportion of *Eurycercus* was also high in the September diet of both storsik and sandsik, indicating that some positive effects of the damming-up phase still remained.

IV. DISCUSSION

Storsik—sandsik

It seems that although the two benthic species have a similar diet, small specimens of the larger storsik have a better adapted ability to feed on large prey than sandsik. In environments where this type of food is available, storsik has a good chance of living sympatrically with sandsik and of dominating in large sizes. The smaller sandsik on the other hand, has a competitive edge with regard to an ability to feed on plankton and in

being more flexible in diet. Sandsik therefore generally dominate numerically over storsik.

The most competitive of the six whitefish species is the blåsik which is not found in Lake Parkijaure. The blåsik has a similar diet to sandsik, but is more planktivorous. In lakes where blåsik has built up a population, sandsik are few in number and the storsik may consequently be more dense (SVÄRDSON 1979).

The diets of sandsik and storsik respectively, are more differentiated in Parkijaure than in other investigated lakes. Generally chironomid larvae is a common prey for both species. In some cases the prey may be superabundant and the segregation between the species is low. In other cases, however, the lake habitat and hence the prey fauna, is probably less complex and so the food ranges overlap. After becoming a reservoir, Lake Parkijaure has lost the large larvae of caddisflies and Mayflies and the proportion of chironomid larvae has increased in the food of sandsik and storsik. Their diets now overlap more than before and the competition

Table 4. *The age-distribution of the whitefish species in the catch before impoundment in 1970 and after impoundment in 1975.*

Age	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	
Storsik	1970	—	—	22	22	23	13	10	7	2	—	1
	1975	—	1	4	6	11	13	14	6	5	1	—
Sandsik	1970	1	9	42	23	17	8	—	—	—	—	—
	1975	—	36	37	15	10	2	—	—	—	—	—
Planktonsik	1970	—	5	50	39	6	—	—	—	—	—	—
	1975	—	44	51	3	1	1	—	—	—	—	—
Aspsik	1970	—	—	4	4	2	13	24	28	12	6	2
	1975	—	2	4	3	4	11	6	3	3	1	—

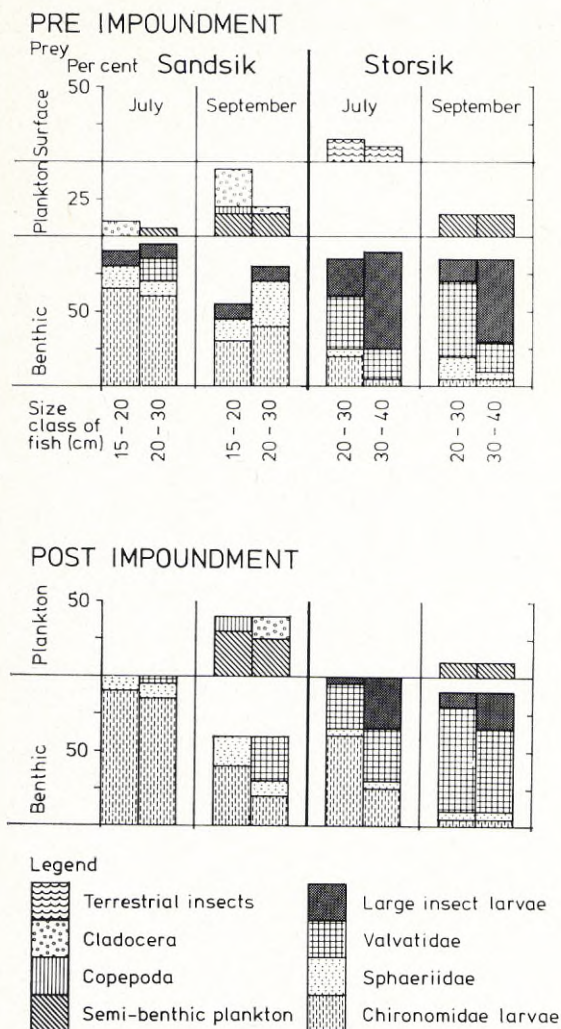


Fig. 8. The diets of the two benthic whitefish species after impoundment. Large insect larvae had decreased and the proportion of Chironomidae larvae increased in the diet.

has sharpened. Possibly the storsik will become fewer in number relative to sandsik in the future.

Sandsik and the planktivorous whitefish pair

In midwater the catch was composed of young sandsik, planktonsik and aspsik. All had fed on plankton. The sandsik had fed exclusively on cladocerans and *Cyclops* captured above the bottom, while planktonsik and aspsik fed on calanoid copepods as well. This suggests that the sandsik is less well adapted for catching plankton

than the planktivorous species, and that its main food niche is benthic.

Aspsik and the benthophagous whitefish pair

Aspsik was partly caught in the same habitat as sandsik above the bottom in the lower part of the littoral zone and in the profundal. In spite of the fact that aspsik dwelt on the bottom, the stomachs contained plankton and surface food. Although aspsik shared the habitat of the benthic whitefish, it did not utilize the same food resource. In most lakes the diets of the benthophagous whitefish and the more planktivorous aspsik is clearly differentiated, even when the habitats overlap. In some lakes, however, benthic prey is also included in the diet of aspsik, and the food composition, as regards the proportion of plankton-surface-benthic prey, therefore differs from lake to lake (LINDSTRÖM and NILSSON 1962). These differences can be explained by the varying availability of certain prey in different lakes. In addition, we now know, that the aspsik is more or less introgressed with whitefish species with few rakers and that the aspsik demes in Sweden form a series of populations with gill raker averages ranging from 45 to 62 (SVÄRDSON 1979). It is quite possible that the gene flow has affected the feeding habits as well, so aspsik with few rakers have a more benthic diet. The 'normal' feeding niche of aspsik is, however, planktivorous.

Planktonsik and aspsik

With the exception of surface food which aspsik took in the height of the summer, the two planktivorous species utilized the same food resources and fed almost entirely on the same zooplankton species. Planktonsik was decidedly the most dominant of the two numerically, and the stomachs were well filled, whereas the stomachs of aspsik were often empty. Aspsik was also caught above the bottom probably while digesting, indicating that aspsik performed vertical movements and dwelt in deeper water in order to save energy. Its reaction to improved food conditions (Fig. 7) was also the strongest.

According to SVÄRDSON's (1979) interpretation of whitefish speciation, planktonsik and aspsik both belong to the peled species group with a common progenitor. The center for the parental

species is the non-glaciated area of eastern Siberia. The planktonic is the older invader and thus better adapted to Scandinavian conditions. The small size of the planktonic seems to be an adaptation for living in cold oligotrophic lakes with a low food ration. In most cases, where the two species live sympatrically, planktonic is dwarfed, but numerically abundant, and the least modified demes of aspsik seem to be the least competitive.

Summing up, the whitefish species in this investigation all had clearly differentiated feeding habits. When studying the diet in detail, it was found that even the most closely related species differed in their feeding habits. In agreement with SVÄRDSON (1979) it is suggested that the feeding preferences have a considerable hereditary component. If the habitat of the lake is varied and the prey fauna is complex, conditions are good for closely related species to live sympatrically. If lakes are impoverished, however, feeding is affected and the better adapted species will dominate. Probably introgression and gene flow will increase simultaneously.

V. ACKNOWLEDGMENTS

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VI. REFERENCES

- FÜRST, M., U. BOSTRÖM and J. HAMMAR. 1980. Effects of introduced *Mysis relicta* on fish in Lake Vojmsjön. *Inform. Inst. Freshw. Res., Drottningholm* (3). 42 p. (In Swedish with English summary.)
- HOLMBERG, A. 1975. Food habits of three species of whitefish, and a qualitative analysis of the zooplankton in Lake Locknesjön (province of Jämtland, Sweden). *Inform. Inst. Freshw. Res., Drottningholm* (5). 29 p. (In Swedish with English summary.)
- LINDSTRÖM, T. 1962. Life history of whitefish young (*Coregonus*) in two lake reservoirs. *Rep. Inst. Freshw. Res., Drottningholm* 44: 113—144.
- 1964. Char and whitefish recruitment in north Swedish lake reservoirs. *Rep. Inst. Freshw. Res., Drottningholm* 46: 124—140.
- 1973. Life in a lake reservoir: Fewer options, decreased production. *Ambio* 11(5): 145—153.
- 1974. Småsikens betydelse för fisket i det vattenkraftsexploaterade, nordsvenska landskapet. *Inform. Inst. Freshw. Res., Drottningholm* (16). 48 p. (In Swedish.)
- and N.-A. NILSSON. 1962. On the competition between whitefish species. p. 326—340. In *The exploitation of natural animal populations*. Eds.: E. D. LeCren and M. W. Holdgate. Brit. Ecol. Soc. Symp., Durham 28th—31st March 1960. Blackwell Scientific Publications, Oxford.
- NILSSON, N.-A. 1958. On the food competition between two species of *Coregonus* in a North-Swedish lake. *Rep. Inst. Freshw. Res., Drottningholm* 39: 146—161.
- 1960. Fluctuations in the food segregation of trout, char and whitefish. *Rep. Inst. Freshw. Res., Drottningholm* 41: 185—205.
- 1963. Interaction between trout and char in Scandinavia. *Trans. Am. Fish. Soc.* 92(3): 276—285.
- 1978. The role of size-biased predation in competition and interactive segregation in fish. p. 303—325. In *Ecology of freshwater fish production*. Ed.: S. D. Gerking. Blackwell Scientific Publications, Oxford.
- and B. PEJLER. 1973. On the relation between fish fauna and zooplankton composition in north Swedish lakes. *Rep. Inst. Freshw. Res., Drottningholm* 53: 51—77.
- SVÄRDSON, G. 1979. Speciation of Scandinavian *Coregonus*. *Rep. Inst. Freshw. Res., Drottningholm* 57. 95 p.
- VOLOSHENKO, B. B. 1973. A comparative analysis of the feeding of underyearlings of the pelyad (*Coregonus peled* (GMELIN)), the broad whitefish (*Coregonus nasus* (PALLAS)) and their hybrids when reared together. *J. Ichtyol. (AFS)* 13(4): 569—576.

The Validity of the Removal Method for Small Populations — Consequences for Electrofishing Practice

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ABSTRACT

The accuracy of the confidence intervals of the removal method (Moran-Zippin's estimator) applied to small populations was investigated by Monte Carlo simulation, using catchabilities in the range of 0.5–0.8 and for 2 and 3 removals.

For the two-sample case, the confidence interval is valid for populations down to 200 for catchabilities from 0.5 to 0.7. For 0.8, a population size of 100 may be tolerated.

For the three-sample case and catchabilities from 0.5 to 0.7, the confidence interval is reasonably well estimated for populations down to about 50. For a catchability of 0.8, the confidence interval tends to be too narrow for populations smaller than 200.

For population sizes above the minimum limits indicated above, the precision is generally acceptable for both cases. For the two-sample case and a catchability of 0.5, the precision may be too low for most applications. The precision is greatly improved, especially for small populations, if an approximately known catchability is used.

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I. INTRODUCTION

The maximum likelihood solution to the removal method of population estimation (MORAN 1951, ZIPPIN 1956, 1958, JUNGE and LIBOSVARSKY 1965, SEBER and LE CREN 1967, SEBER 1973, p. 309–325) is perhaps the method most widely applied to electrofishing, especially in the case of salmonid density assessment in small streams. Apart from purely practical considerations, the utility of the method is determined by its accuracy and precision, and the possibility of calculating these parameters with confidence.

There are two main problems of applying the removal method to electrofishing. The first one is the validity of the assumption of equal catch probability among individuals and effects of deviations from this assumption. This question has

been discussed by JUNGE and LIBOSVARSKY (1965), SEBER and WHALE (1970) and BOHLIN and SUNDSTRÖM (1977), who concluded that unequal catchability would result in a negative bias, the magnitude of which will depend on the catchability distribution among individuals. Few attempts have been made to test the accuracy of the removal under field conditions. BOHLIN and SUNDSTRÖM (1977), however, using natural and semi-natural salmonid populations of known size, found a general underestimation in the magnitude of 15 %, probably as a result of unequal catchability.

The second main problem is the validity of the large-sample normal theory required for accurate confidence limits. In the case of the two-sample method (number of removals=2), SEBER (1973, p. 322) concludes that the method is "satisfactory for $N > 200$ and p not too small", where N is the population size and p the catchability. For the three-sample case, ZIPPIN (1956) came to the conclusion that the large-sample normal theory gave reasonable confidence limits for $N > 200$ and $p=0.4$. In electrofishing, however, the catchability is usually in the range 0.5–0.7, and the populations encountered may sometimes be quite small, especially in the case of older fish or in low-density areas. In view of the frequent use of

electrofishing, the adequacy of the confidence interval in these cases needs further investigation.

This study, therefore, deals with the precision of the removal method and the possibility of calculating this precision with accuracy, and is restricted to conditions frequently encountered in electrofishing surveys. Statistical theory is kept at a minimum, and some consequences of the results are given as recommendations.

II. METHODS

A simple and straight forward way of testing the validity of a method is to carry out numerical experiments under reasonably realistic conditions and to compare the actual outfall with the known parameters. In the present study, the successive catches of the removal method were simulated using Monte Carlo technique and assuming equal catchability among individuals, and by applying different p values (0.5, 0.6, 0.7, 0.8) and N values (400, 200, 100, 75, 50, 25) for each run. For each of the 24 parameter combinations, the two-sample as well as the three-sample method was used. 100 replicas were carried out, in each case estimating the population size (\bar{N}), the standard error (\widehat{SE}), the catchability (\hat{p}) and the 95 % confidence limits. To obtain the validity of these estimates, their means over the 100 replicas were calculated

$$\left(\bar{N} = \frac{\sum \bar{N}}{100}, \widehat{SE} = \sqrt{\frac{\sum (\widehat{SE}^2)}{100}}, \bar{p} = \frac{\sum \hat{p}}{100}\right),$$

and the number of confidence intervals not including the known population size noted.

The following estimators were used.

Two-sample case (SEBER and LE CREN 1967)

$$\bar{N} = C_1^2 / (C_1 - C_2)$$

$$\bar{N}_k = \bar{N} - \hat{q}(1 + \hat{q}) / \hat{p}^3 \text{ (allowance for statistical bias)}$$

$$\hat{p} = (C_1 - C_2) / C_1$$

$$\hat{q} = 1 - \hat{p}$$

$$\widehat{SE} = \frac{C_1 C_2}{(C_1 - C_2)^2} \cdot \sqrt{C_1 + C_2}$$

$$95\% \text{ conf. limits} = \bar{N} \pm 2 \widehat{SE}$$

Three-sample case (JUNGE and LIBOSVARSKY 1965)

$$\bar{N} = \frac{6X^2 - 3XY - Y^2 + Y \cdot \sqrt{Y^2 + 6XY - 3X^2}}{18(X - Y)}$$

$$\hat{p} = \frac{3X - Y - \sqrt{Y^2 + 6XY - 3X^2}}{2X}$$

where $X = 2C_1 + C_2$, and

$$Y = C_1 + C_2 + C_3$$

$$\widehat{SE} = \sqrt{\frac{\bar{N}(1 - \hat{q}^3) \hat{q}^3}{(1 - \hat{q}^3)^2 - 9 \hat{p}^2 \hat{q}^2}}$$

where $\hat{q} = 1 - \hat{p}$

$$95\% \text{ confidence limits} = \bar{N} \pm 2 \cdot \widehat{SE}$$

III. RESULTS

The outcome of the simulations are displayed in Table 1 and 2. The following can be noted.

For the two-sample case, SEBER's conclusion mentioned above is supported. The standard error and the confidence limits are valid for populations > 200 . For $p=0.8$, however, a population size down to 100 may be tolerated. Further, the precision is not so good for $p=0.5$. In practice, thus, the results indicate that use of the two-sample method should be restricted to populations > 200 and catchabilities ≥ 0.6 .

For the three-sample case and $p=0.5$ to 0.7, the standard error is reasonably well estimated for populations down to 75, and the confidence interval valid for populations to about 50. For $p=0.8$, the confidence interval tends to be too narrow for populations below 200, probably because of the skewed sampling distribution when the total sampling fraction is large (ZIPPIN 1958). Further, the precision of the three sample case is generally quite good. For $p=0.5$, however, the precision may be too low for small populations. The three-sample method, thus, can normally be used quite safely for populations down to about 50.

Sometimes, however, the populations may be considerably smaller than the minimum limits indicated above, e.g. in the case of older fish. One way to handle this problem is to apply a p value estimated from a larger population, e.g. a pooled population from several occasions, and to estimate the size of the small population N_s as $\bar{N}_s = T / (1 - \hat{q}^k)$

where T is the total catch of the small population for the k removals, and $\hat{q} = 1 - \hat{p}$, where \hat{p} is the estimated catch probability for the large population. The precision of \bar{N}_s depends of \bar{N}_s and the precision of \hat{p} . If the size of the large population

Table 1. Simulation results of the two-sample case, based on 100 replicas. The estimates, given as percentage of the parameter values, are shown together with the percentage of failing runs and the percentage of successful confidence limits (Conf. l.). xxx denotes results for which not even the magnitude is nearly correct.

	N	\bar{N} (% of N)	\bar{N}_k (% of N)	SE	\widehat{SE} (% of SE)	P	\bar{P} (% of p)	Failed (%)	Conf. l. (%)
p=0.5	400	102	99	54.2	101	0.5	100	0	96
	200	102	98	36.3	83	„	101	0	92
	100	105	92	36.9	63	„	100	0	90
	75	114	63	89.4	37	„	96	0	88
	50	124	xx	xxxx	xx	„	100	2	84
	25	123	xx	xxxx	xx	„	114	4	71
p=0.6	400	100	100	22.1	94	0.6	100	0	94
	200	101	99	18.0	101	„	101	0	91
	100	103	99	15.4	85	„	99	0	90
	75	111	xx	xxxx	xx	„	97	0	93
	50	106	93	16.4	60	„	99	0	90
	25	118	xx	xxxx	xx	„	102	0	81
p=0.7	400	100	100	12.7	95	0.7	99	0	95
	200	101	100	9.65	95	„	99	0	93
	100	102	100	7.77	93	„	99	0	91
	75	102	100	8.73	89	„	99	0	90
	50	103	99	7.79	72	„	98	0	92
	25	104	82	15.3	34	„	102	1	90
p=0.8	400	100	100	6.58	105	0.8	99	0	95
	200	100	100	4.81	106	„	100	0	95
	100	101	100	3.81	100	„	99	0	95
	75	101	100	3.34	95	„	99	0	92
	50	102	100	4.29	91	„	100	0	88
	25	102	98	3.51	56	„	101	0	90

is sufficient (say more than a hundred), its p value not too low (say more than 0.5), and the number of removals at least 3, the standard error of this p estimate will be quite low. If so, a rough idea of the precision of the removal method also for small populations may be obtained by considering the p value exactly known and applying binomial theory. In this case the standard error of the small population is estimated as

$$\widehat{SE}_s = \sqrt{\bar{N}_s \hat{q}^k / (1 - \hat{q}^k)}$$

where, as above, k is the number of removals for the small population. In Table 3. this standard error is calculated for k=3 and for some values of p and N_s. The result indicates a quite reasonable precision of the removal method even for small populations. In practice, when the p value is estimated rather than known, the precision will be less good. It can, however, be shown from

BOHLIN (1981, eq. 6) that the effect of an "estimated" p value is negligible in the situations most frequently encountered, and consequently that the expression for \widehat{SE}_s above may be practically useful.

IV. RECOMMENDATIONS

In the usual range of catchabilities, the three-sample method is recommended for general use in favour of the two-sample method because of its acceptable precision and accurate confidence limits down to a population size of about 50. The two-sample method may be used when the catchability is 0.6 or larger, and for populations larger than 200. For populations below the limits above, estimates of reasonable precision may be obtained by applying a catchability estimate derived from a larger population.

Table 2. Simulation results of the three-sample case, based on 100 replicas. The estimates, given as percentage of the parameter values, are shown together with the percentage of failing runs and the percentage of successful confidence limits (Conf. l.). xxx denotes results for which not even the magnitude is nearly correct.

	N	\bar{N} (% of N)	SE	\widehat{SE} (% of SE)	p	\hat{p} (% of p)	Failed (%)	Conf. l. (%)
p=0.5	400	100	15.8	98	0.5	100	0	94
	200	100	10.5	109	"	100	0	94
	100	103	9.52	114	"	99	0	95
	75	103	8.98	110	"	100	0	89
	50	104	9.19	136	"	99	0	94
	25	108	8.59	xxx	"	103	0	90
p=0.6	400	100	8.86	98	0.6	100	0	95
	200	100	6.09	102	"	100	0	94
	100	101	4.11	117	"	99	0	94
	75	101	4.13	105	"	100	0	96
	50	101	3.19	121	"	100	0	94
	25	103	2.62	144	"	100	0	92
p=0.7	400	100	4.42	113	0.7	99	0	98
	200	100	3.45	95	"	100	0	91
	100	100	2.26	107	"	100	0	93
	75	100	2.08	108	"	100	0	94
	50	100	1.40	136	"	100	0	95
	25	104	5.91	xxx	"	99	0	85
p=0.8	400	100	2.38	92	0.8	100	0	97
	200	100	1.63	96	"	100	0	94
	100	100	1.19	98	"	100	0	90
	75	100	1.15	85	"	101	0	89
	50	100	0.95	87	"	101	0	80
	25	102	0.86	86	"	100	0	64

Table 3. Theoretical standard errors for varying populations N from 10 to 25 and varying catchabilities p from 0.55 to 0.75, assuming p known and the number of removals 3.

N	Catch probability p				
	0.55	0.60	0.65	0.70	0.75
25	1.58	1.31	1.12	0.83	0.63
20	1.42	1.17	0.95	0.75	0.56
15	1.23	1.01	0.82	0.65	0.49
10	1.00	0.83	0.67	0.53	0.40

V. ACKNOWLEDGMENTS

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VI. REFERENCES

BOHLIN, T. 1981. Methods of estimating total stock, smolt output and survival of salmonids using electro-

fishing. *Rep. Inst. Freshw. Res. Drottningholm* 59: 5-14.

— and B. SUNDSTRÖM. 1977. Influence of unequal catchability on population estimates using the Lincoln Index and the removal method applied to electrofishing. *Oikos* 28(1): 123-129.

JUNGE, C. O. and J. LIBOSVARSKY. 1965. Effects of size selectivity on population estimates based on successive removals with electrical fishing gear. *Zool. Listy* 14(2): 171-178.

MORAN, P. A. P. 1951. A mathematical theory of animal trapping. *Biometrika* 38: 307-311.

SEBER, G. A. F. 1973. The estimation of animal abundance and related parameters. Griffin, London. 506 p.

— and E. D. LE CREN. 1967. Estimating population parameters from catches large relative to the population. *J. Anim. Ecol.* 36: 631-643.

— and J. F. WHALE. 1970. The removal method for two and three samples. *Biometrics* 26: 393-400.

ZIPFIN, C. 1956. An evaluation of the removal method of estimating animal populations. *Biometrics* 12: 163-169.

— 1958. The removal method of population estimation. *J. Wildl. Manag.* 22: 82-90.

Electro-Fishing for Salmonids in Small Streams – Aspects of the Sampling Design

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ABSTRACT

Using simple random sampling of stream sections and applying the removal method to each of the sections, the spatial distribution of juvenile sea trout (*Salmo trutta*) in two small streams was studied using electrofishing. The distributions were contagious with a coefficient of variation in the magnitude of 0.7 for trout of age I+ and older. On the basis of the results, the approximate sampling intensity required to reach varying levels of precision of the mean density estimate was calculated. Stratification with respect to biotope improved the precision. The effect of varying number of removals in each section was studied by numerical experimentation, suggesting a negligible gain in precision for a number of removals exceeding 3, and a small gain from 2 to 3 removals in the case of large total populations. The consequences of the results are put forward in the form of recommendations.

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I. INTRODUCTION

Stock assessment of salmonids in small streams has received a great deal of attention since the 1950's when electrofishing came into general use. In addition to fisheries biology and management, environment monitoring has presently become one of the main fields for the application of this method in many parts of the world.

By applying the removal method (see e.g. SEBER 1973, p. 309–327) to electrofishing, reasonably accurate estimates of the salmonid density in sections of small streams may be obtained (BOHLIN and SUNDSTRÖM 1977). Unfortunately, however, the possibility of making useful statements about the entire stock, e.g. the population size in a stream, is negatively influenced by the large spatial variation in population density and

other parameters in streams. Since the aim of most electrofishing surveys is to make such statements, information of the spatial variation of population parameters and its consequences for stock analysis is necessary for the planning of an electrofishing survey. In this paper we will give some practical guide-lines concerning the sampling design and the fishing effort required to reach a reasonable precision of the population density. The recommendations and conclusions made are based on data from 88 quantitative electrofishings on sea-trout populations in two small streams in SW Sweden. Some statistical considerations, based on the work of BOHLIN (1981), are given as an introduction.

II. STATISTICAL ERRORS OF THE POPULATION DENSITY ESTIMATE

Often or usually a complete stream survey by electrofishing is impossible or impracticable to carry out even in comparatively small streams because of the time-consuming field work. If so, statements about the stock must be based on the information contained in a sample of stream sections, drawn at random out of the total number of potential sections of the stream. The accuracy and precision of these statements about the stock

is then determined by two error components: error 'within sections' and error 'between sections'.

The 'within sections' error is generated from the population estimation within each section, usually and conveniently obtained by the removal method. For a section i in a stream, the population size estimate \hat{x}_i and its sampling variance $V(\hat{x}_i)$ can be computed by the ZIPPIN (1956) estimators or their modifications (see SEBER 1973, p. 309—327). This variance is proportional to the population size x_i and decreasing with an increasing number of removals and with an increasing catchability of the fish.

The 'between sections' error is caused by the fact that the population size varies among different parts of the stream and that only a few such parts can be studied. Say that a stream is made up by a total of N sections of approximately the same length or area, and that only n of these are studied. If these n sections are drawn at random, we can estimate the mean population density per section as

$$\bar{x} = \frac{\sum x_i}{n} \quad (1)$$

The precision of this estimate depends on the number of sections studied and the variation of fish density in the stream, and also by the total number of sections in the stream. The sampling variance can be expressed as

$$\hat{V}(\bar{x}) = \frac{\hat{V}(x)}{n} \left(1 - \frac{n}{N}\right) \quad (2)$$

where $\hat{V}(x)$ is an estimate of the variation in fish density among sections, calculated as

$$\hat{V}(x) = \frac{\sum (x_i - \bar{x})^2}{n - 1} \quad (3)$$

Thus, if the spatial variation $V(x)$ of a population is known or can be estimated, and if the size of the stream N is known, it is possible to get an idea of the number of sections (n) required to reach a reasonably low value of the sampling variance $V(\bar{x})$. The formulas (1)—(3), however, are strictly valid only if the population sizes x_i of the studied sections are exactly known. As stated above, this is usually not the case since the x_i 's are estimated as \hat{x}_i rather than known, which makes the situation a bit more complicated. The following approach was adopted.

Consider eq. (3), expressing the variance $V(x)$ 'between sections'. Now instead of the true x_i values we have a number of observations \hat{x}_i which are more or less precise. The variance $V(\hat{x})$ among these observations are likely to be somewhat larger than $V(x)$, since the former also includes a 'within sections' variance component. Further, this 'within sections' variance can be estimated by the removal method (for details, see BOHLIN 1981, Appendix 2). Since the variances are additive this leads to an opportunity to estimate the unknown $V(x)$ 'between sections':

$$\hat{V}(x) = \hat{V}(\hat{x}) - (\text{'within sections' variance}) \quad (4)$$

In the sections below, we used this relation in two ways. Using field data we estimated the variance components in the case of applying 3 removal fishings in each section. Accepting the estimated $V(x)$ value as a parameter, we then went on to investigate the total sampling variance for varying number of removals and varying number of stream sections sampled.

III. STUDY AREAS AND FIELD WORK

Two small softwater streams, Jörlandaån and Norumsån, in SW Sweden, were chosen for this study. Catchment areas are 39 km² and 15 km², respectively. The water flows are characterized by heavy fluctuation with peaks usually in autumn/winter and minimum flow in summer. The mean flows are 0.4 and 0.15 m³s⁻¹, respectively. The sea trout *Salmo trutta* is the most abundant fish species together with the minnow *Phoxinus phoxinus*. The streams flow through shallow valleys dominated by arable and pasture land, mainly marine clay and postglacial moraine.

The field work was organized in the following way. The streams (or in one case part of the stream) were divided into N sections of equal length. From these sections a sample of n sections were drawn at random for the purpose of electrofishing and according to the scheme below:

Sample	Stream	Section length	N	n
1	Jörlanda 1981, autumn	100 m	92	20
2	Jörlanda 1980, upper part, spring	50 m	43	20

Sample	Stream	Section length	N	n
3 a	Jörlanda 1974, autumn	50 m	184	14
b	Jörlanda 1975, autumn	50 m	184	11
c	Jörlanda 1976, autumn	50 m	184	8
4	Norum 1981, autumn	100 m	86	15

In each section of each sample the number of juvenile sea trout in different age classes was estimated in the following way. Using a DC electrofishing gear, 400 V, 3 removals were carried out in a standardized way. The catches were divided by the length frequency to classes approximately equal to age classes. For each of the classes the successive catches were pooled over the n sections. For these pooled populations the catchability p was estimated using the ZIPPIN estimator. The population size x_i in each section was then estimated as

$$\hat{x}_i = \frac{T_i}{1 - \hat{q}^k}$$

where T_i is the total catch for the k removals in section i , and $\hat{q} = 1 - \hat{p}$.

IV. RESULTS

Estimated variance components in the case of 3 removal fishings

Using the approach outlined above, we started the analysis by calculating the 'between' and 'within' sections variances for our largest samples (sample 1, 2 and 4). The result is shown in Table 1. It is clearly evident that in these samples the 'within sections' variance is negligible in comparison to the large 'between sections' variance. The implication is that the removal method in these cases may be considered to yield practically exact estimates of the population size in the different sections. For practical purposes, therefore, formulas (1), (2) and (3) above may be used for a further analysis.

Accepting the conclusion above we ignored the 'within sections' variances and treated all samples as 'normal' ones. Frequency distributions of the

Table 1. Variance components of samples 1, 2 and 4.

Sample No and age class	Variance among sections	Variance within sections
1. I+	898.4	2.22
II+ and older	89.9	0.79
2. I+	631.8	3.18
II+ and older	305.7	0.61
4. 0+	28,347	13.75
I+	42.2	0.47
II+ and older	135.6	0.11

large samples 1 and 2 are given in Fig. 1. The population means, standard deviations and coefficients of variation for all samples are shown in Table 2.

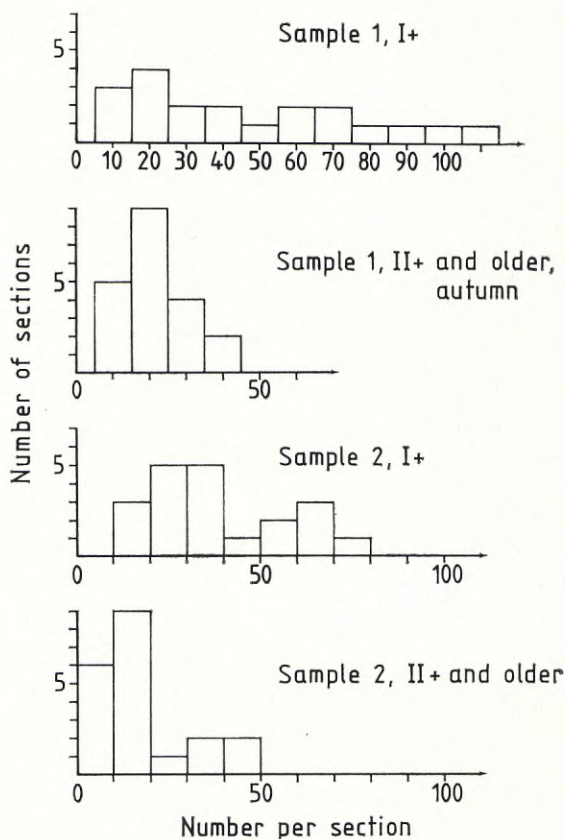


Fig. 1. Frequency distribution of the number juvenile trout per section for sample 1 and 2. Note the large variation, especially for trout of age class I+.

Table 2. *Estimates of the mean density \bar{x} , the standard deviation s , and the coefficient of variation $C=s/\bar{x}$ for juvenile trout in different age classes and samples. n is the sample size.*

Sample No	0+				I+				II+ and older			
	n	\bar{x}	s	C (%)	n	\bar{x}	s	C (%)	n	\bar{x}	s	C (%)
1, Jörlanda	—	—	—	—	20	48.0	30.0	63	20	21.6	9.51	44
2, Jörlanda	—	—	—	—	20	38.9	25.2	65	20	17.7	17.5	99
3, Jörlanda (a)	11	58.3	62.9	108	14	54.3	27.8	51	14	9.57	4.88	51
(b)	11	148	103	70	11	16.1	14.4	89	14	3.91	3.29	84
(c)	7	118	85.7	73	8	59.7	29.3	49	8	4.53	3.31	73
4, Norum	15	190	165	87	15	22.6	24.2	107	15	17.5	11.7	67

All populations appear to be contagious ($s^2 \gg \bar{x}$). Although the coefficients of variation vary among the samples, there is a tendency towards larger values for the smaller fish. For I+ fish and older the coefficient of variation is varying around 0.7.

If the coefficient of variation is of the same magnitude in other streams, we can use the value from the streams studied as a preliminary generalization to get an idea of the sampling intensity required to reach given levels of precision. In Table 3 the result of this computation is shown. In most practical applications, the standard error, to be useful, should not be allowed to exceed 10 % of the mean. It is evident from Table 3 that even this moderate precision would require a large number of electrofishings, larger than what seems to be commonly applied. Until further data on the spatial variation of salmonids in small streams is available, we propose that Table 3 should be used as an aid for a preliminary determination of the sampling intensity required in cases when mean density of salmonids is of interest.

Stratified random sampling

One of the reasons for the large population variation is probably the heterogeneous environ-

ment in streams. Stratification with respect to biotope might then reduce the variation and increase the efficiency as compared with simple random sampling. The effect of stratification, using standard technique (see *e.g.* SNEDECOR and COCHRAN 1967, p. 520—523), was studied in samples 1 and 2.

The upper part of Jörlandaån, from which sample 2 was drawn, is naturally divided into two very different biotope types: canalized parts through fields, and natural, mostly fast-flowing and stony sections. In sample 2 we therefore stratified the stream into canalized parts (C) and natural biotopes (N).

In sample 1, covering the entire stream, the grounds for stratification were less obvious. Two biotope extremes, however, could be recognized: hardbottom, mainly fast-flowing parts, and soft-bottom, mainly slow-flowing parts. Between these categories fell, however, a number of sections of intermediate character. We chose to divide the stream into three strata: hard-bottom (H), soft-bottom (S) and intermediate (HS).

In Table 4 a comparison between random sampling and stratified sampling is shown. The reduction of variances was considerable in sample 2, resulting in a 50 % lower standard error as

Table 3. *The approximate number of sections in a sample required to reach various levels of precision, assuming a coefficient of variation of 0.7, simple random sampling of sections, and 3 removals in each section.*

Level of precision (standard error: mean)	Total number of stream sections (N)						
	10	25	50	75	100	200	∞
5 %	10	22	40	54	66	100	200
10 %	8	17	25	30	33	40	50
20 %	6	8	10	11	11	12	12

compared with the simple random sampling. In sample 1 the gain in precision was less pronounced for older fish but still considerable for age class I+.

In order to reach a required level of precision, the results thus indicate that the sampling effort can be reduced if stratification is applied. The gain in precision, however, may vary widely between streams of different character and depends largely on how well 'high density' and 'low density' biotopes can be recognized.

How many removal fishings?

So far we have ignored the 'within sections' error generated by the use of removal method, which seemed justified in the cases above. Further, we have shown that, in the case of 3 removals, a large number of time consuming electrofishings may be required to get a reasonably good precision of the fish density estimate. A question of interest is therefore if it would pay, in terms of total field work, to apply only 2 removals and to add a few extra sections.

Although we have not found any simple analytical solution to this problem, an idea of the effect of the number of removals may be obtained by numerical experimentation, using the values from our field work as parameters. The catchability was assumed = 0.60 and the coefficient of variation = 0.70. Trying a number of different mean densities and values of N (total number of sections in the stream) we calculated the standard error for varying sample size and number of removals. The result of one such simulation is shown in Fig. 2. It can be noted that the precision in the case of 3 removals is approximately as good as in the case of a very large number of removals, which is not surprising in view of the results of the preceding sections. It is perhaps more notable that the loss in precision from 3 to 2 removals is rather small and approximately balanced by an increase in sample size by 2 or 3 sections. Other combinations of parameters yielded similar results. For small populations, however, (N small, mean density small) the loss in precision from 3 to 2 removals was larger.

The conclusion to be made from the results above is that it is probably not worthwhile to apply more than 3 removals when estimating

Table 4. Effects of stratification in samples 1 and 2. SE_{st} is the standard error after stratification, and SE the standard error as obtained by simple random sampling. \bar{x} , s, n and N has their usual meaning, with subscript referring to stratum.

	Sample 1		Sample 2	
	I+	II+	I+	II+
Stratum	H	H	N	N
\bar{x}_1	84.30	18.2	53.0	26.80
s_1	22.43	2.65	13.70	10.90
n_1	5	5	8	8
N_1	21	21	20	20
Stratum	S	S	C	C
\bar{x}_2	30.33	28.2	29.40	11.6
s_2	14.06	8.02	9.40	3.50
n_2	7	7	12	12
N_2	39	39	23	23
Stratum	HS	HS		
\bar{x}_3	40.84	17.90		
s_3	26.01	10.90		
n_3	8	8		
N_3	26	26		
\bar{x}_{st}	46.6	22.60	40.37	18.70
SE_{st}	3.84	1.60	2.00	1.45
SE	5.88	1.86	4.12	2.86
% improvement	35	14	52	49

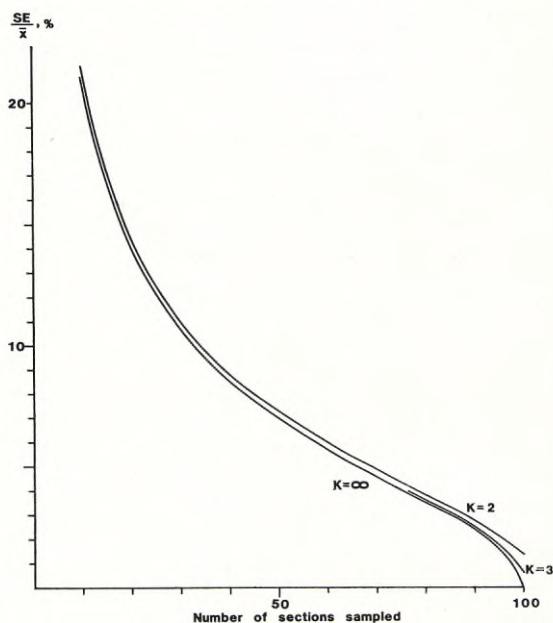


Fig. 2. The theoretical standard error, given as percentage of the mean density, for different number of removals (K) and number of sections sampled. In this case the total number of stream sections is $N=100$, the mean density $\bar{x}=50$, and the coefficient of variation 0.7. The catchability is assumed to be 0.6.

mean density. For large populations (large mean density, many sections) 2 removals may be considered. It should also be noted that other solutions may be practicable, e.g. to apply several removals in sections with many fish and fewer in sections with low density. The main impression from the results above is in any case that the large problem is to overcome the error raised by the large spatial variation of fish in streams. An increase in the number of removals has thus little effect on the precision, and a large number of sections will probably be necessary in any case.

V. CONCLUSIONS AND RECOMMENDATIONS

- 1) In most cases, electrofishing in small streams should be carried out in such a way that inferences about the *stock* can be made. The parameters of main interest are usually mean density, population standard deviation, and total stock size.
- 2) In cases when total stream sampling is impracticable, simple or stratified random sampling of stream sections is suitable.
- 3) To make a preliminary decision of the sampling intensity required, Table 3 may be consulted. The standard error should normally not be allowed to exceed 10 % of the mean.
- 4) In the usual range of catchabilities (0.5 and above), 3 removal fishings is the maximum number to be recommended. 2 removals may be sufficient in the case of large total populations.

VI. ACKNOWLEDGMENTS

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VII. REFERENCES

- BOHLIN, T. 1981. Methods of estimating total stock, smolt output and survival of salmonids using electrofishing. *Rep. Inst. Freshw. Res. Drottningholm*, 59: 5—14.
- and B. SUNDSTRÖM. 1977. Influence of unequal catchability on population estimates using the Lincoln Index and the removal method applied to electro-fishing. *Oikos* 28 (1): 123—129.
- SEBER, G. A. F. 1973. The estimation of animal abundance and related parameters. Griffin, London. 506 p.
- SNEDECOR, G. W. and G. C. COCHRAN. 1967. Statistical methods, sixth edition. The Iowa State University Press, Ames. 593 p.
- ZIPPIN, C. 1956. An evaluation of the removal method of estimating animal populations. *Biometrics* 12: 163—169.

The Population of Brown Trout, (*Salmo trutta* L.) in Some Regulated Lakes in Southern Norway

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ABSTRACT

A total of 49 trout lakes exposed to different levels of water impoundment, were studied with respect to catch per effort, length — age composition, and several growth parameters. The results were based on sampling with standard net series once in each lake. There were slight negative correlations between catch per effort, mean weight and growth with increasing water amplitude. However, due to great variations in values at all regulation levels, the correlations were not significant. As for age and length composition, there was a tendency of increasing share of older and smaller fish with increasing impoundment.

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I. INTRODUCTION

Various ecological programs have been initiated to study the impact of fluctuating water level upon the freshwater life. A serious reduction in both qualitative and quantitative food production of bottom fauna in the littoral zone of regulated lakes has been documented (STUBE 1958, GRIMÅS 1961, 1962, NILSSON 1961).

Concerning the fish fauna in these reservoirs, the most essential changes are connected with the growth rate of the fish (RUNNSTRÖM 1952, 1955, 1964). RUNNSTRÖM (1964) states that it was natural to associate these changes with that of the regulated lakes. At the present time more than one half the total freshwater area in Norway has been impounded for the purpose of producing hydroelectric power (AASS 1973). The majority of these reservoirs are oligotrophic lakes inhabited by brown trout (*Salmo trutta* L.) only.

Since 1972 a team under the direction of the Directorate for Wildlife and Freshwaterfish has carried out general studies of the effect of impoundment on fish populations in order to find the best way of managing the different reservoirs with respect to fish production. A total of about 200 lakes with different levels of regulation and fish species composition in Southern Norway are included in the project (GARNÅS, HESTHAGEN and GUNNERØD 1981). The lakes were more or less randomly chosen and thus vary with respect to altitude, size and water quality. In the present paper we will discuss if any general trends can be pointed out between density and growth rates of the trout populations and increasing lake regulation, based on the results from the project.

II. MATERIAL AND METHODS

The results are based on 49 lakes where brown trout is the only species and pH \geq 5.5. However, minnow (*Phoxinus phoxinus* (L.)) may occur in some of the lakes. Fig. 1 shows the reservoirs' distribution with respect to impoundment, altitude and planting of trout. Twenty of the lakes were only influenced by regulation as a result of impoundment in the watershed, leading to reduced water flow. The water amplitude of the other lakes varies between 1—30 m annually. Planting of trout is carried out in 22 of the lakes.

The results include about 1,000 brown trout

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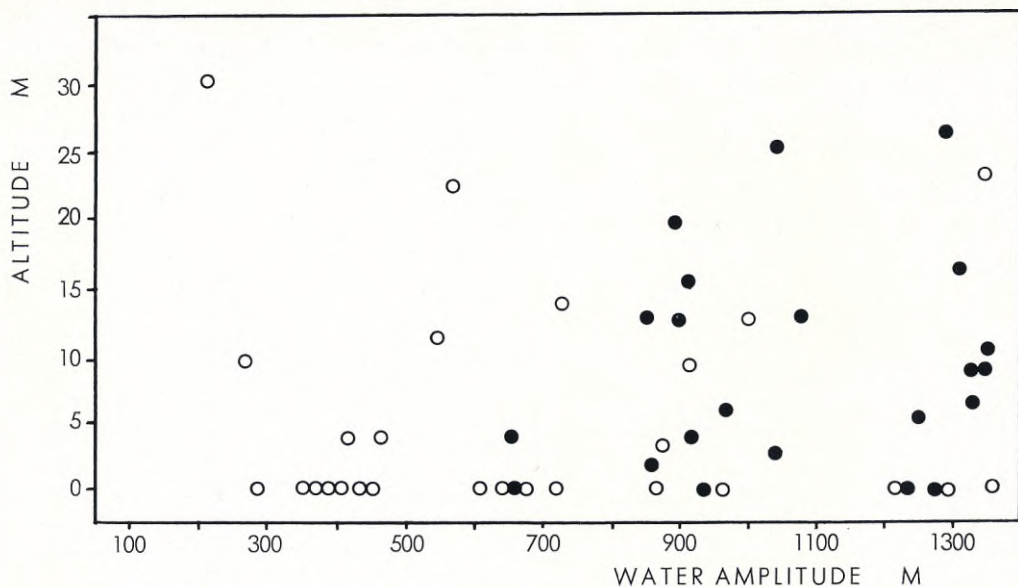


Fig. 1. Distribution of the 49 brown trout lakes included in this study according to water amplitude and altitude. Solid marks are lakes where planting of trout occurs.

specimens, collected from 1972—79. Fish were caught by using standard gill-net series consisting of different mesh sizes (mm): 52—45—40—35—29—26—21—21. This series has nearly the same efficiency on all trout sizes between 18 and 49 mm (JENSEN 1977). The gill netting was mainly carried out in August. Each locality was sampled from one to four nights using one to four series each night.

Fish length was defined as total length. The trout were aged by using scale analysis. In back calculation of the growth rate, isometric growth between fish and scales was assumed.

Age and length composition of the catch was defined in relation to the 40 % fractile of group length 22 cm (L_{22}) and group age 4 years (A_4). If 40 % or more of the sample was < 22 cm, the individuals in the population were considered small. Opposite if less than 40 % of the samples was < 22 cm, the individuals were defined as large. Age composition was grouped in young and older fish, also according to the 40 % fractile. Age and length composition was then divided in four different groups:

- I $L_{22} >$, $A_4 >$ 40 % — Small and younger fish
- II $L_{22} >$, $A_4 <$ 40 % — Small and older fish

- III $L_{22} <$, $A_4 <$ 40 % — Large and older fish
- IV $L_{22} <$, $A_4 >$ 40 % — Large and younger fish

The growth parameters ultimate length (L_{∞}) and growth coefficient (k) in von Bertalanffy's growth equation were expressed as length increment (ΔL) from age 4 to age 6.

III. RESULTS

In Fig. 2 catch per net series, the mean fish weight, and the three different growth parameters are plotted against water amplitude. Average values of catch per series, mean weight and ΔL in each regulation category are shown in Table 1.

Results show great variations in catch per series amongst different lakes at all levels of regulation. However, there was a slight negative correlation between catch per series and increasing regulation ($r = -0.21$). Catch per series in lakes uninfluenced by regulation and those regulated from 6—15 m was significantly higher than in lakes which exhibited a water amplitude of 1—5 m ($P < 0.05$ Wilcoxon's two sample test). There were no significant differences in catch per series between the other regulation categories ($P > 0.05$).

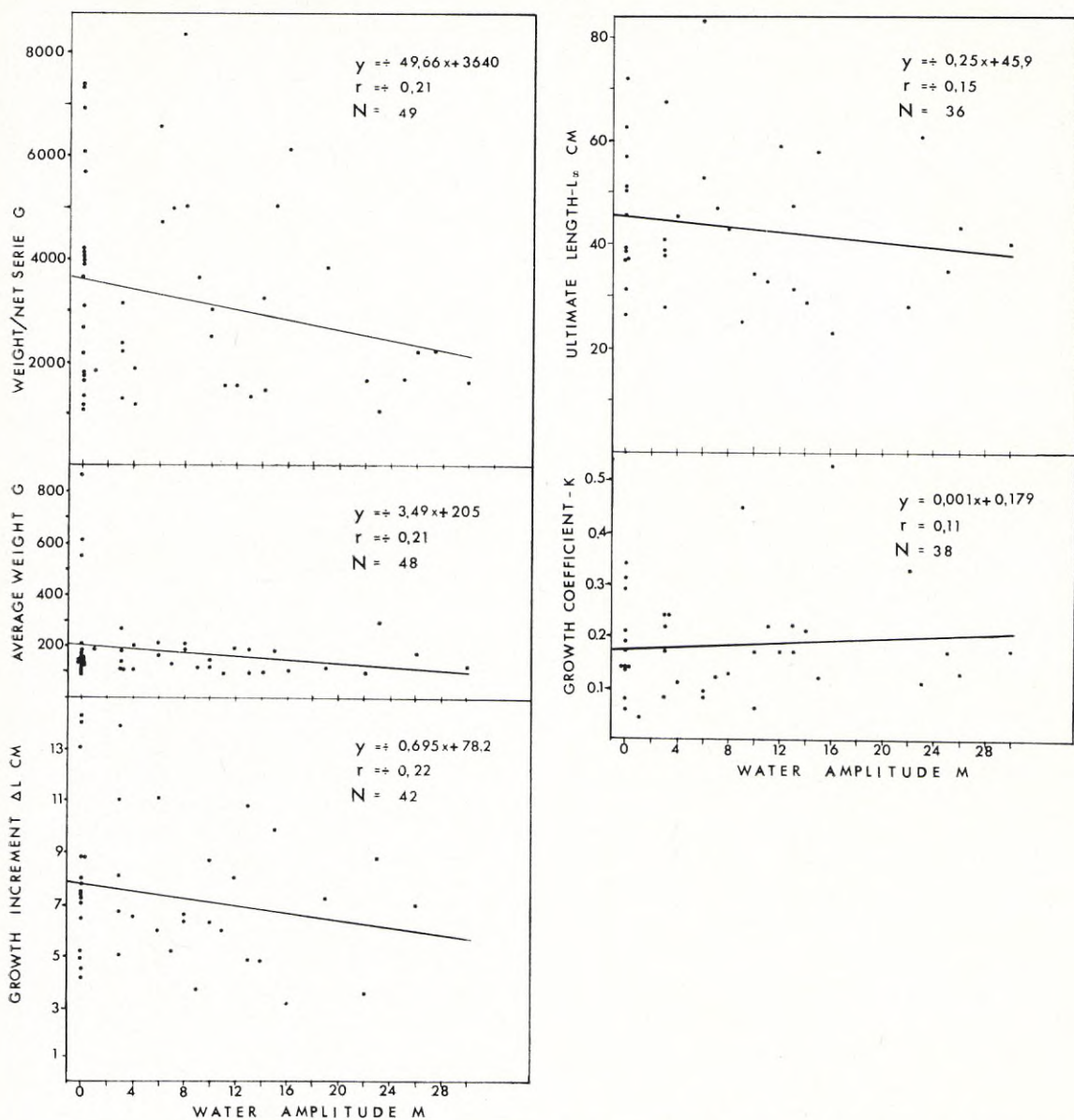


Fig. 2. Catch per effort, average weight, and three different growth parameters of brown trout with respect to water amplitude. N =number of lakes, r =correlation coefficient.

Mean fish weight was reduced with increasing water amplitude. There was a slight negative correlation between the two parameters ($r = -0.21$). However, there was no significant difference between average mean weight in the four regulation categories ($P > 0.05$), due to variations in mean weight at all water amplitudes.

Length increment (ΔL) showed a minor negative correlation with increasing water amplitude ($r = -0.22$). No significant differences were noted between average ΔL in the four regulation categories ($P > 0.05$). Growth expressed as ultimate length (L_{∞}) and growth coefficient (k) was reduced with increasing water amplitude. Respec-

Table 1. Catch per effort, mean weight and length increment (ΔL) of brown trout in lakes of four regulation levels. Wilcoxon's two sample test is used to test the differences of the parameters between the regulation groups.

Regulation level	Test group	Mean weight/series (g)	Standard error of mean	No. of lakes	Mean weight (g)	Standard error of mean	No. of lakes	$\Delta L(L_6-L_4)$ mm	Standard error of mean	No. of lakes	
0 m	1	3693	461	20	225	48	19	84	8	12	
1-5 m	2	2144	287	8	165	20	8	82	13	6	
6-15 m	3	3779	565	14	152	11	14	72	6	14	
≥ 15 m	4	2591	678	7	140	27	7	55	8	7	
Test 1 vs 2: 0.01 < P < 0.02				Test 1 vs 4: 0.05 < P < 0.1				Test 1 vs 4: 0.05 < P < 0.1			
1 vs 4: 0.05 < P < 0.1				Other: P > 0.2				Other: P > 0.2			
2 vs 3: 0.02 < P < 0.05											
Other: P > 0.2											

tively, a slight negative ($r = -0.15$), and slight positive (0.11) correlation between these two parameters was found.

The number of small and young fish decreased with increasing water amplitude for lakes regula-

ted 0-15 m (Fig. 3). However, for lakes where the water amplitude exceeded 15 m, the frequency of small and young fish was even higher than in lakes only slightly influenced by regulation. The occurrence of small and older fish increased

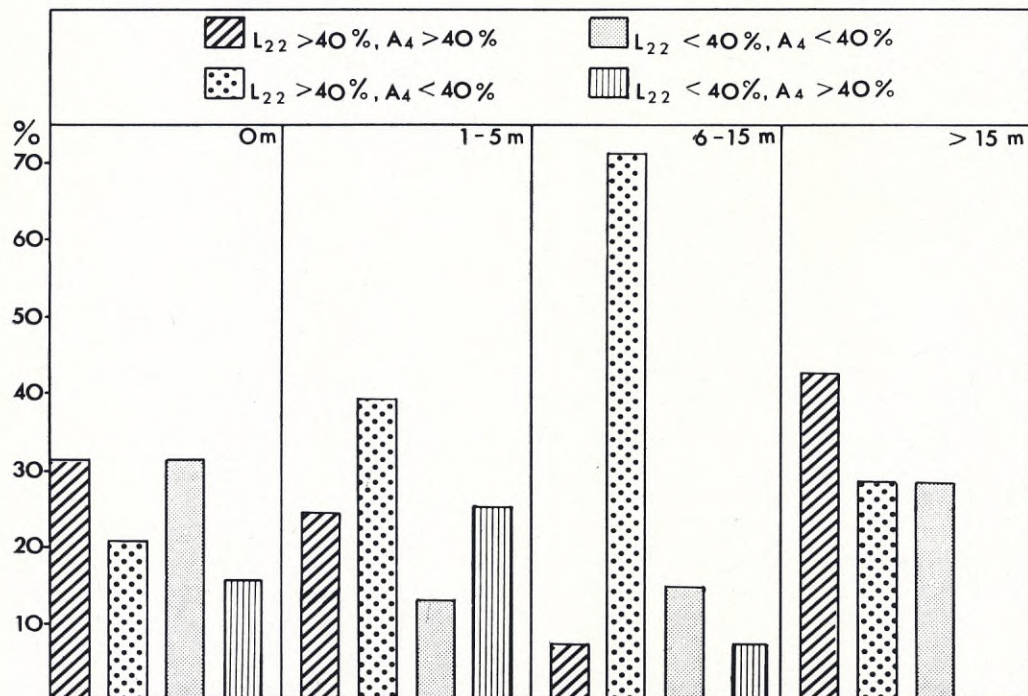


Fig. 3. Age and length composition according to the 40% fractile of group length 22 cm and group age 4 years of brown trout populations in lakes of four different regulation levels.

distinctly with increasing regulation level, making up some 71 % of the catch in lakes regulated 6—15 m.

The group of large and older fish did not show any special trend in relation to regulation level, though they were most numerous in lakes influenced by high amplitude. For regulated lakes there was a pronounced reduction in number of young and large fish related directly to increasing regulation level. In about 25 % of the lakes regulated 1—5 m, the population consisted of young and large fish. In lakes with a water amplitude exceeding 5 m, there was only one population which exhibited this length and age composition.

IV. DISCUSSION

Catch per effort (C/E) using standard net series is thought to be a useful method for classifying fish density in lakes (JENSEN 1979). However, because sampling was carried out only once in each lake, the results can only supply description of the fish population at a given instant. But the results may give an indication of age and length distribution of the fish population in each lake. Hence, it will show if the density of fish is too high or low in relation to available food.

The results indicated a slight tendency of reduced C/E with increasing impoundment. However, there were great variations in this parameter at all water amplitudes. Besides impoundment, different lake elevation, size and fishing intensity of the lakes may influence the results.

Production of bottom fauna is known to be reduced with increasing altitude (RADDUM 1974). Comparing C/E amongst different regulation categories is therefore dependent of even distribution with respect to altitude of the lakes. However, no significant difference in distribution between lakes in each regulation category with regard to elevation was found ($P > 0.05$, Wilcoxon's two sample test).

Lake size may also influence production of food animals. Small lakes are usually more shallow than large ones, resulting in a higher production of bottom animals. According to JENSEN (1979) C/E was lower in lakes larger than 500 ha. However, the lakes in this investigation

were generally smaller than 500 ha, thus error due to varying surface area was thought to be negligible.

Impounded lakes are exposed to fluctuating fishing pressure. In some of these lakes net fishing, the dominating fishing gear used in Norwegian lakes, is complicated by roots and bushes never having been removed from the shore line. In other lakes, fishing pressure will fluctuate because of varying interest from local fishermen. Differences in fishing intensity will have great influence both on density and growth condition of the trout populations. The combined effects of fishing pressure and varying water amplitude are corroborated in this investigation.

There is also known to be a short term positive effect on fish populations in a period after impoundment, due to increased nutrients available from the flooded areas (RUNNSTRÖM 1952, FROST 1956). The lakes studied in this investigation have all been regulated for more than ten years. This factor can therefore most likely be excluded, because the effect generally lasts for eight to ten years (AASS 1973).

As for growth rates of the trout populations, both growth increment ($L_6 - L_4$), ultimate length (L_∞) and growth coefficient (k) indicated decreasing growth with increasing water amplitude.

Growth reduction is known to occur for both trout and char in impounded lakes (RUNNSTRÖM 1952, STUBE 1958). Impoundment will lead to disruption between population density and available food, resulting in growth reduction (RUNNSTRÖM 1964). However, when judging changes in growth of fish in regulated lakes, separation caused by impoundment and that from changes in population density is needed. If population density becomes reduced as a result of increased natural mortality, emigration (BORGSTRÖM 1973), or loss of spawning areas, the growth can remain unchanged in spite of the reduction in available food.

The results of the age and length composition in the present study, indicated an increasing share of small and older fish with increasing water amplitude. This indicates reduced fish production with increasing impoundments, based on the populations' turnover rate (P/B). Increased average age, reduced growth and thus reduced

production with increased impoundment, may, however, also be caused by less effective fishing, which leads to reduced amount of available food because of increased competition (RUNNSTRÖM 1951).

Planting of trout in impounded lakes is carried out in large numbers to compensate for reduced natural propagation caused by impoundment. In 64 % of the lakes regulated more than 5 m, planting of trout occurs regularly. However, these lakes contain mostly smaller fish (< 22 cm). This fact indicates that planting of excessive number of trout in relation to available food and existing fishing pressure cause reduced fish growth and production. Also, in extensively regulated lakes where no planting occurs, fish populations are dominated by smaller fish. Generally, natural propagation seems to be sufficient to sustain the fish stocks in these lakes.

At present time the lakes contain mostly trout populations of slow growth and small individuals. To increase fish production, there is a need for a more keen adjustment to food production. This can be achieved by reducing the stock by increasing the fishing intensity and reduce the mean age of first capture through regulation of mesh size of the nets.

The prevailing population structure and growth pattern of brown trout in the lakes studied are probably caused by a combination of water impoundment, low fishing pressure and excessive planting.

V. ACKNOWLEDGMENTS

We would like to express our thanks to Dr. TOR B. GUNNERØD who has been the leader of the project and to all the persons who have collected the data which this work is based on.

VI. REFERENCES

- AASS, P. 1973. Some effects of lake impoundments on salmonids in Norwegian hydroelectric reservoirs. *Acta Univ. Upsalensis Diss. Sci.* 234: 1—14.

- BORGSTRÖM, R. 1973. The effect of increased water level fluctuation upon the brown trout population of Mår vann, a Norwegian reservoir. *Norweg. J. Zool.* 21: 101—112.
- FROST, W. 1956. The growth of brown trout (*Salmo trutta* L.) in Haweswater before and after the raising of the level of the lake. *Salm. Trout Mag.* 148: 266—274.
- GARNÅS, E., T. HESTHAGEN and T. B. GUNNERØD. 1981. Regionale undersøkelser i regulerte vatn i Sør-Norge fra 1972—1979. *DVF-Reguleringsundersøkelse, Rapp.* 3. 62 p. (In Norwegian.)
- GRIMÅS, U. 1961. The bottom fauna of natural and impounded lakes in northern Sweden (Ankarvattnet and Blåsjön). *Rep. Inst. Freshw. Res., Drottningholm* 42: 183—237.
- 1962. The effect of increased water level fluctuations upon the bottom fauna i Lake Blåsjön, Northern Sweden. *Rep. Inst. Freshw. Res., Drottningholm* 44: 14—41.
- GULLAND, J. A. 1973. Manual of methods for fish stock assessment. Part 1. Fish population analysis. *FAO Manuals Fish. Sci.* 4. 155 p.
- JENSEN, J. W. 1979. Catch per effort with standard series of bottom gill nets on brown trout and char in Norwegian lakes. *Gunneria* 31: 1—36. (In Norwegian with English summary.)
- JENSEN, K. W. 1977. On the dynamics and exploitation of the population of brown trout, *Salmo trutta* L. in Lake Øvre Heimdalsvatn, southern Norway. *Rep. Inst. Freshw. Res., Drottningholm* 56: 18—69.
- NILSSON, N.-A. 1961. The effect of water-level fluctuations on the feeding habits of trout and char in the lakes Blåsjön and Jormsjön, North Sweden. *Rep. Inst. Freshw. Res., Drottningholm* 42: 238—261.
- RADDUM, G. G. 1974. Benthosundersøkelser i vann i Røldal/Suldal feltet 1970—1972. *Rapp. Lab. Ferskvannskol. Inlandsfiske, Bergen* 13. 127. (In Norwegian.)
- RUNNSTRÖM, S. 1952. The population of trout, *Salmo trutta*, Linné, in regulated lakes. *Rep. Inst. Freshw. Res., Drottningholm* 33: 179—198.
- 1955. Changes in fish production in impounded lakes. *Proc. Int. Ass. Theor. Appl. Limn.* 12: 176—182.
- 1964. Effects of impoundment on the growth of *Salmo trutta* and *Salvelinus alpinus* in Lake Ransasen (Swedish Lappland). *Verh. Internat. Verein. Limnol.* 15: 453—461.
- STUBE, M. 1958. The fauna of a regulated lake. *Rep. Inst. Freshw. Res., Drottningholm* 39: 162—224.

Tagging and Release of Atlantic Salmon Smolts (*Salmo salar* L.) in the River Rana, Northern Norway

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ABSTRACT

From 1970 to 1974 a total of 18,592 one- and two-years-old reared smolts were tagged with Carlin tags and released in different parts of the River Rana, Northern Norway. Releases in the upper parts of the river yielded lower recapture rates than releases in the lower parts. Two-years-old smolts tend to mature at an earlier sea age than one-year-old smolts. But it was impossible to estimate the impact of genetic differences between the two groups, and different responses to environmental factors during the sea period. Recaptures were reported from large areas of the Norwegian sea and the Norwegian coast. 13.5 % of the recaptures, however, were reported from the River Rana. Straying to other rivers was common, 17.6 % of the river recaptures were reported from nearby rivers. Taking into account tagging mortality and nonreported tags, some of the experiments were considered to be profitable. This was not the case when considering the river recaptures alone.

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ranching (THORPE 1980), but in Norway yield calculations must be available before eventual decisions to release large amounts of smolts are taken.

The aim of this paper is to summarize results from several releasing experiments of Atlantic salmon smolts in the River Rana, Northern Norway. The emphasis is on growth, migration and yield calculations.

I. INTRODUCTION

For many years reared smolts of Atlantic salmon *Salmo salar* L. have been released in and outside Norwegian rivers. Some results from these releases have been summarized by ROSSELAND (1965, 1979). Summaries of Norwegian smolt releases and recaptures can be found in the 1980 report to ICES from The Working Group on North Atlantic Salmon. Recently HANSEN (1980 a and b) has presented results from smolt releases in River Vefsna, Northern Norway and River Glomma, S.E. Norway.

Such experiments can give information on the biology of salmon, for instance migrations and growth. They also furnish information on the most important fishing areas and the fishing gears involved.

There has been an increasing interest in salmon

II. DESCRIPTION OF THE WATERCOURSE

The River Rana is fed by tributaries in the Svartisen glacier area and Lake Northern Bjøllavatn in the north and some smaller river systems close to the border of Sweden in the east. The river runs into the sea at Mo i Rana (Fig. 1). The watercourse has a catchment area of 3,790 km² (BERG 1964).

There are two important salmon ladders in the river. One is situated in the 7 m high Kobbfors waterfall about 11 km from the sea, and the other is located in the 29 m high Reinfors about 2 km above the Kobbfors waterfall. Salmonids can migrate up the main river as far as the Raufjellfors waterfall about 55 km from the sea. 1,124 km² of the catchment area is dominated by the glacier

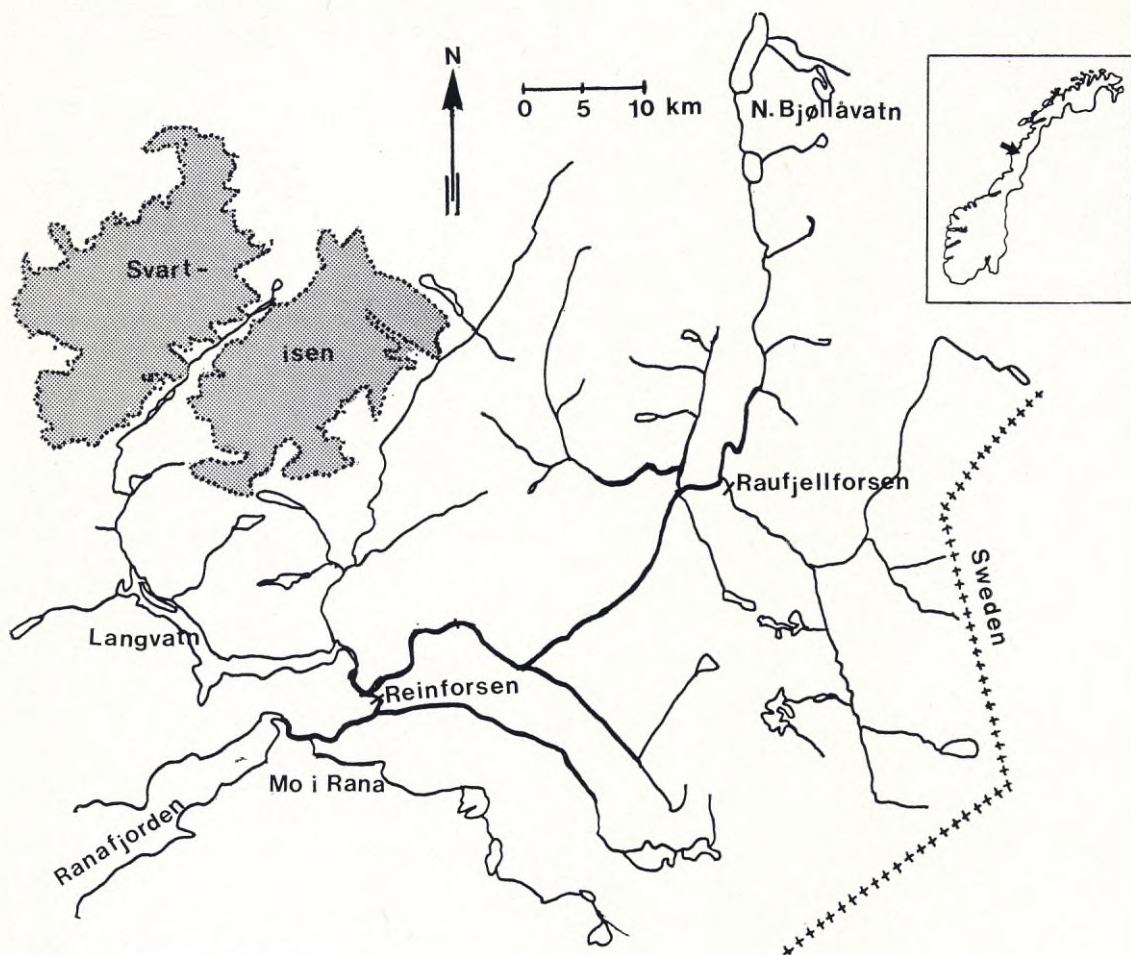


Fig. 1. The River Rana watercourse.

Svartisen. Because of the low water temperature and the high turbidity in these parts of the river system it is doubtful whether salmon ascend here (BERG 1964). No juvenile salmon were found in this part of the river in 1976 by electrofishing (JOHNSEN 1978).

In 1923 a small hydro-electric power station came into effect at Reinfors. The output was increased from 1964, and the maximum power production in the watercourse is now estimated at about 468 MW.

Both Atlantic salmon, brown trout *Salmo trutta* L. and anadromous char *Salvelinus alpinus* (L.) are found in the river. In the lower parts of the river, stickleback (*Gasterosteus aculeatus* L. and

flounder (*Platichthys flesus* (L.)) are occasionally found (JOHNSEN 1978).

Further information about the river system is given by BERG (1964) and JOHNSEN (1978).

Fig. 2 shows the salmon catches in the River Rana based on Reports from the Central Bureau of Statistics of Norway. Although these figures are uncertain, they probably express the main trends.

In the 1960's there was a peak in the catches reaching a level of 1,200 to 1,400 kg. At the beginning of the 1970's the catches dropped to about 200–400 kg. The catches later increased considerably to approximately 3,000 kg. Simultaneously an increasing number of salmon were registered in the Reinfors' fish ladder (JOHNSEN

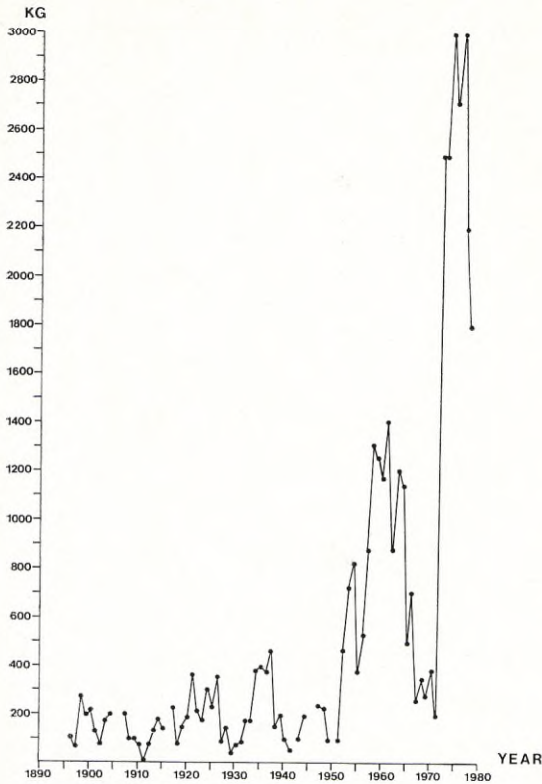


Fig. 2. Salmon catches in the River Rana since 1896 (From Central Bureau of Statistics, Oslo, Norway.)

1978). Starting in 1967 Rana Hydro-Electric Company were ordered to release 30,000 smolts yearly. This level was eventually reached in 1972.

III. MATERIAL AND METHODS

From 1970 to 1974 a total of 18,592 tagged salmon smolts were released in different parts of the River Rana (Table 1). The majority of the smolts were released close to the mouth of the river, but one group was released at Reinfors on June 20, 1972. A total of 2,500 smolts were released above Reinfors.

The smolts were reared at Rana Hydro-Electric Company's hatchery. The parent fish were caught in the sea. It is therefore likely that the offspring are a crossbreed between different river-populations.

The smolts were anaesthetized with Sandoz MS 222, measured (total length) to the nearest full cm and tagged with Carlin tags (CARLIN 1955). The smolts were tagged some weeks before release. They were transported by truck and released directly into the river.

In 1971 a group of small one-year-old smolts and a group of 54 very large two-year-old smolts were released on October 27 and 29. There were no recaptures from the first release, but three adults were recaptured from the second release. Due to special circumstances connected with autumn releases we found it appropriate not to include these two groups in the total computations.

All catches were reported by anglers and commercial fishermen. If the fish weight was not reported, mean weight at actual sea age has been used in the yield calculations.

Table 1. Survey of the tagged and released smolts in River Rana. The smolts were reared at the Rana Hydro-Electrical Company's hatchery.

Age years	Year of release	Date of release	Place of release	No. released	Mean smolt length (cm ± SD)
1	1970	June, 17	Below Reinfors	4965	18.0 ± 1.2
1	1971	October, 27	Below Reinfors	600	14.0 ± 1.0
2	1971	October, 29	Below Reinfors	54	30.0 ± 2.7
2	1972	May, 18—19	Below Reinfors	478	19.0 ± 1.4
2	1972	June, 20	Below Reinfors	1999	16.0 ± 1.8
1	1973	May, 15	Below Reinfors	500	16.7 ± 1.4
1	1973	May, 15	Above Reinfors	500	16.8 ± 1.4
1	1973	June, 5	Below Reinfors	1000	16.4 ± 1.3
1	1973	June, 5	Above Reinfors	1000	16.5 ± 1.4
1	1973	June, 20, 29	Below Reinfors	1000	16.4 ± 1.1
1	1973	June, 29	Above Reinfors	1000	16.5 ± 1.3
1	1974	June, 14	Below Reinfors	3500	17.7 ± 1.8
2	1974	June, 14	Below Reinfors	1996	18.1 ± 3.0

Table 2. *Distribution of the recaptures of tagged salmon smolts released in the River Rana during the years 1970—74. The 1971 releases are not included in the total computations. (A=Above Reinforc, B=Below Reinforc).*

Year of release	Date of release		No. recaptured as smolts	Recaptured as adults						Total no. recaptures	% recapture
				Norw. home waters	Norw. s.	River Rana	Other rivers	Unknown			
1970	June, 17	(B)	19	96	9	11	4	7	127	2.6	
1971	October, 27	(B)	0	0	0	0	0	0	0	0	
1971	October, 29	(B)	1	0	2	0	1	0	3	5.6	
1972	May, 18—19	(B)	0	16	2	0	0	0	18	3.8	
1972	June, 20	(B)	4	80	10	16	4	1	111	5.6	
1973	May, 15	(B)	0	5	0	0	0	0	5	1.0	
1973	May, 15	(A)	0	7	0	0	0	0	7	1.4	
1973	June, 5	(B)	1	40	2	5	0	0	47	4.7	
1973	June, 5	(A)	1	8	0	4	1	1	14	1.4	
1973	June, 20, 29	(B)	0	29	1	8	2	1	41	4.1	
1973	June, 29	(A)	4	11	1	3	0	1	16	1.6	
1974	June, 14	(B)	13	24	0	7	1	1	33	0.9	
1974	June, 14	(B)	2	22	2	7	1	2	34	1.7	
Total			44	338	27	61	13	14	453	2.5	

IV. RESULTS AND DISCUSSION

Distribution of the recaptures

Table 2 shows the recaptures from the different releases 1970—74. We could not detect any systematic difference between groups and year of release with regard to geographical distribution. The recaptures have therefore been pooled and the geographical distribution is shown in Fig. 3.

In 1973, one-year-old smolts were released both above and below Reinforc on three separate occasions. The release made May 15 resulted in no significant difference in the total adult recapture rate when comparing the two groups. But for the releases made June 5 and June 20—29 the recapture rate for fish liberated below Reinforc was significantly higher ($p < 0.01$) than for the group liberated above. This suggests a greater mortality of the smolts released in the upper parts of the river, and the data agree well with experiments done in River Vefsna and River Glomma (HANSEN 1980 a and b).

There was a considerable variation in the recapture rate between different years. It was especially high for the smolt released below Reinforc on June 20, 1972. In 1974 two groups

consisting of one- and two-year-old smolts were released on June 14. The two-year-old smolts had approximately twice the recapture rate of one-year-old smolt. A Wilcoxon signed rank test showed a significant ($p=0.01$) difference in recapture rate between smolt lengths smaller than 25 cm for the two age groups. For two-year-old smolts released in 1974, 56 % of the total number recaptured were recaptured as mature grilse, as opposed to 25 % for the one-year-old smolt. This may help to explain the lower recapture rate for the one-year-old smolt. However, it is impossible to estimate the impact of genetic differences between the two groups and the different responses to environmental factors during the sea period. RITTER (1975) and BAILEY *et al.* (1980) found that two-year-old smolts resulted in a higher proportion of grilse than one-year-old smolts which is supported by the present data. But NAEVDAL *et al.* (1979) in their fish farm experiments presented results contrary to these.

Most recaptures have been reported from northern Norwegian coastal waters (Fig. 3), both far north and far south of the River Rana, indicating that the salmon have different migrating routes towards their home river. The geographical

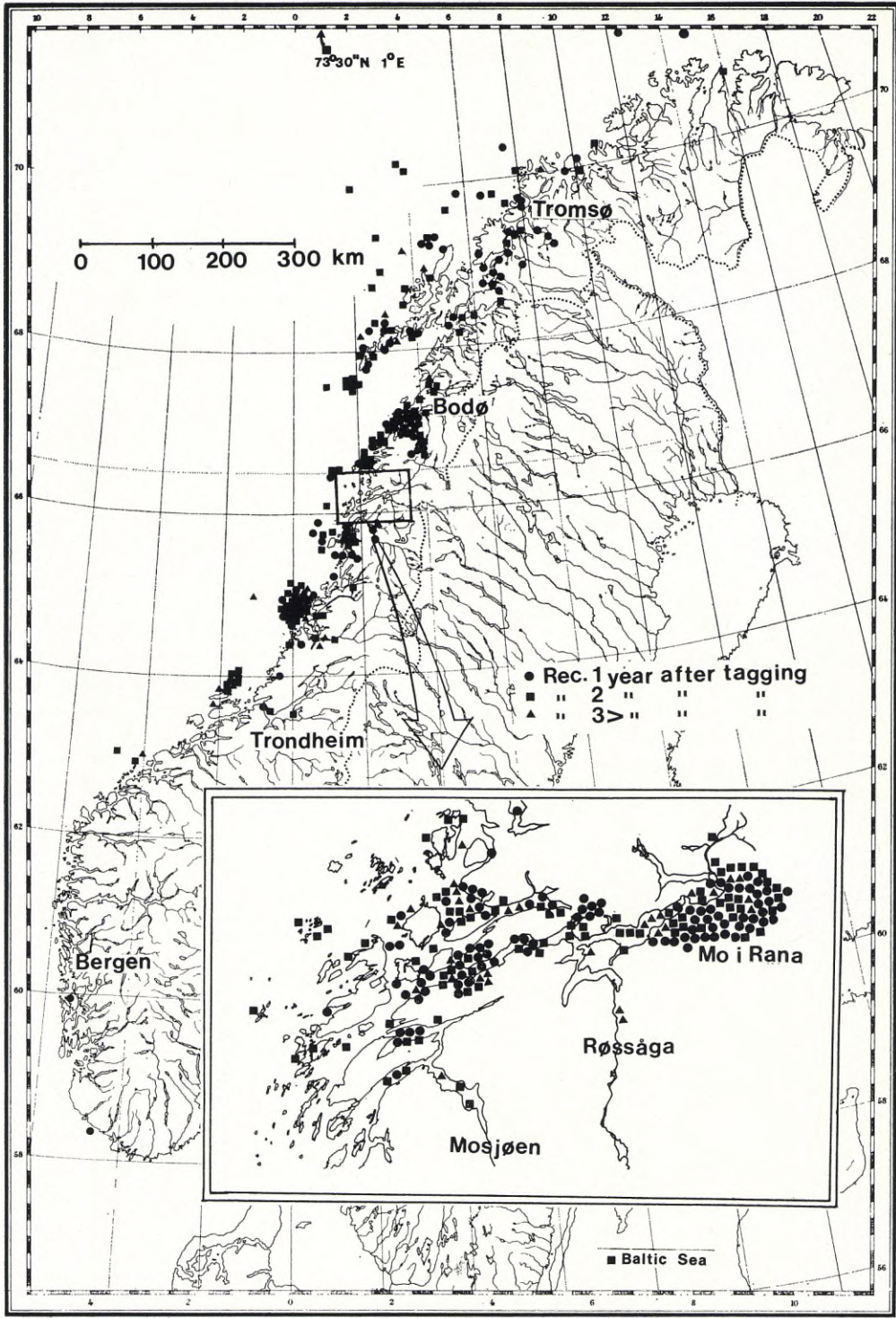


Fig. 3. Geographical distribution of recaptured adult salmon.

Table 3. *Numbers, weight and mean weight of the salmon caught 1—3 years and more after release in the River Rana. 1971 not included in the total computations. (A=Above Reinforc, B=Below Reinforc.)*

Year of release	Date of release		1 year after release			2 years after release			3 years and more after release			Total		
			No.	kg	Mean w.	No.	kg	Mean w.	No.	kg	Mean w.	No.	kg	Mean w.
1970	June, 17	(B)	59	133.6	2.26	48	233.9	4.87	20	145.3	7.27	127	512.8	4.04
1971	October, 27	(B)	0	0	0	0	0	0	0	0	0	0	0	0
1971	October, 29	(B)	1	1.3	1.3	1	—	—	1	—	—	3	—	—
1972	May, 18—19	(B)	8	21.1	2.64	10	53.7	5.37	0	0	0	18	74.8	4.16
1972	June, 20	(B)	53	131.5	2.48	55	306.6	5.57	3	19.1	6.37	111	457.2	4.12
1973	May, 15	(B)	3	9.7	3.23	1	4.1	4.10	1	6.4	6.40	5	20.2	4.04
1973	May, 15	(A)	4	11.6	2.90	2	10.6	5.3	1	7.6	7.60	7	29.8	4.26
1973	June, 5	(B)	17	40.4	2.38	20	97.4	4.87	10	74.1	7.41	47	211.9	4.51
1973	June, 5	(A)	5	16.5	3.30	4	16.0	4.00	5	37.3	7.46	14	69.8	4.99
1973	June, 20, 29	(B)	13	33.1	2.55	19	90.8	4.78	9	72.9	8.10	41	196.8	4.80
1973	June, 29	(A)	6	11.5	1.92	8	32.0	4.00	2	24.2	12.10	16	67.7	4.23
1974	June, 14	(B)	8	15.1	1.89	18	77.0	4.28	7	44.2	6.31	33	136.3	4.13
1974	June, 14	(B)	19	45.1	2.37	8	37.2	4.65	7	54.3	7.76	34	136.6	4.02
Total			195	469.2	2.41	193	959.3	4.97	65	485.4	7.47	453	1913.9	4.22

distribution also gives a picture of the most important exploitation areas. Most of the home water recaptures were taken by bag-, drift-, bend- and setnets, while the bulk of recaptures from international waters were taken by long-line. One recapture has been reported from the Baltic Sea, but it has not been possible to check the validity of this observation.

Only 16.3 % of the total recaptures were reported from freshwater, which strongly indicates heavy sea fishing pressure on the River Rana salmon. Straying was very common and 13 of the 74 river recaptures (17.6 %) were reported from rivers other than the River Rana. Most of the strayers, however, were reported from nearby rivers.

BERG (1977), who tagged wild salmon smolts in the River Vardnes, Northern Norway had a total of 83 recaptures as adults from 1,384 smolts tagged. 71 were recaptured in the sea, and of the 12 river recaptures only 5 were recaptured in the home river. Reared smolts released in the relatively large River Vefsna, some distance south of the River Rana yielded 54 river recaptures 8 of which were from other rivers (HANSEN 1980 a). Releases of smolts reared near Trondheim in the large River Glomma, S.E. Norway had fewer

strayers, only 5 of 201 river recaptures were reported from rivers other than the river of release (HANSEN 1980 b). Similarly in the Baltic, an average of only 2 % of the salmon entered rivers other than their native ones (CARLIN 1969).

Yield

The recapture rates are gross underestimates. One contributory factor is that a large number of recaptures are not reported.

SAUNDERS and ALLEN (1967) had a higher recapture rate of fin-clipped wild smolts than smolts tagged with modified Carlin tags. They also suggested that survival to the adult stage was much higher for unmarked smolts than for tagged and fin-clipped fish. Preliminary results from a tagging experiment with wild smolts in the River Imsa, S.W. Norway gave return rates of 2.4 %, 3.0 % and 6.0 % for Carlin-tagged, adipose fin-clipped and unmarked fish (HANSEN 1980 a). Straying and tag loss can contribute in explaining the difference between unmarked and marked fish, but higher mortality due to handling and marking might be the main explanation. In Iceland ISAKSSON and BERGMAN (1978), working with reared smolts, showed a 1.6 return of micro-tagged fish for each Carlin-tagged, indicating that use of

Table 4. The value of the recaptures. The first hand value is based on the following prices given for gutted salmon by Fremstad A/S, Trondheim in week 24 1980: 1—3 kg kr. 25 per kg, 3—5 kg kr. 32 per kg, 5—7 kg kr. 40 per kg, 7—9 kg kr. 50 per kg and > 9 kg kr. 60 per kg. (A=Above Reinforc, B=Below Reinforc).

Age	Year of release	Date of release		No of kg recaptured per 1,000 smolts re-released	First hand value (N. kr) of the recaptures	First hand value per smolt re-released
One-year old	1970	June, 17	(B)	103	13157	2.65
	1973	May, 15	(B)	40	591	1.18
	1973	May, 15	(A)	60	906	1.81
	1973	June, 5	(B)	212	7063	7.06
	1973	June, 5	(A)	70	2372	2.37
	1973	June, 20—29	(B)	197	6663	6.66
	1973	June, 29	(A)	68	2069	2.07
	1974	June, 14	(B)	39	4355	1.24
		Total			92	37176
Two-years old	1972	May, 18—19	(B)	156	2292	4.80
	1972	June, 29	(B)	229	13990	7.00
	1974	June, 14	(B)	68	4432	2.22
		Total			149	20714

Carlin tags underestimates the true survival to the adult stage.

Table 3 gives the number, weight and mean weights of the recaptures distributed over different years after release. Most salmon matured after one or two years in the sea, but recaptures of two-sea-year-old salmon yielded in total twice as much with regard to weight. A substantial number of salmon were also caught three or more years after release, and the total weight of these was approximately equal to the grilse group. The mean weight for grilse was 2.4 kg, and the mean weights for salmon caught after 2 and 3 years or more in the sea were respectively 5.0 and 7.5 kg.

The value of the recaptures is given in Table 4. The first hand value is based on the following prices given for gutted salmon by Fremstad A/S, Trondheim for week 24, 1980: 1—3 kg NKr. 25, 3—5 kg NKr. 32, 5—7 kg NKr. 40, 7—9 kg NKr. 50 and salmon larger than 9 kg were paid NKr. 60 per kg. As anglers and fishermen report the round weight of the salmon a weightloss of 10 % has been calculated for gutted salmon. In total based on reported recaptures the yield per 1,000 smolts released was 92 kg for one-year-old smolts and 149 kg for two-year-old smolts. This cor-

responds to first hand values of NKr. 2.76 and 4.63 per smolt released respectively.

Since the yields from the different releases show great variations many factors are involved. Some of these are selection of breeding fish, age at maturity and growth, or smolt qualities such as degree of smoltifying, size, age and condition. Factors with regard to release such as locality, time, transport, releasing techniques and environmental factors, for instance, nutrition and predation are also important.

In Norway at present the production price for a one-year-old and a two-year-old smolt can be estimated to about Nkr. 4.— and Nkr. 8.— respectively. If we assume that the true yield is actually double what the total reported recaptures show, some of the experiments can be considered to be profitable when catching expenses are not included. When considering the river recaptures alone all experiments were unprofitable. In Norway similar yields are reported from tagging experiments from River Vefsna and River Glomma (HANSEN 1980 a and b). In the Baltic, however, higher total yields are reported, but most recaptures are reported from the feeding areas (e.g. CARLIN 1969, LARSSON *et al.* 1979).

ROSSELAND (1979) who summarized some results from Norwegian releasing experiments concluded that in spite of some exceptions, the results were rather discouraging although with increasing salmon prices this may change. But as shown in Norway (ROSSELAND 1969, GUNNERØD and KLEMETSEN 1976, JENSEN 1979), and other important salmon producing countries (e.g. ÍSAKSSON 1980, LARSSON 1980, RITTER and CAREY 1980) improvements in the factors which determine the survival of salmon will undoubtedly contribute increasing the yield of Atlantic salmon smolt releases.

V. ACKNOWLEDGMENTS

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VI. REFERENCES

- BAILEY, J. K., M. I. BUZETA and R. L. SAUNDERS. 1980. Returns of three year classes of sea ranched Atlantic salmon of various river strains and their hybrids. *ICES C.M.* 1980/M: 9. 10 p.
- BERG, M. 1964. Nord-Norske lakseelver. Johan Grundt Tanum Forlag, Oslo. 300 p. (In Norwegian with English summary.)
- 1977. Tagging of migrating salmon smolts (*Salmo salar* L.) in the Vardnes river, Troms, Northern Norway. *Rep. Inst. Freshw. Res., Drottningholm* 56: 5—11.
- CARLIN, B. 1955. Tagging of salmon smolts in the River Lagan. *Rep. Inst. Freshw. Res., Drottningholm* 36: 57—74.
- 1969. The migration of salmon. *Rep. Swed. Salm. Res. Inst.* (4): 14—22.
- GUNNERØD, T. B. and C. E. KLEMETSEN. 1976. To forsøk med transport og utsetting av laksesmolt i sjøer. Trondheim og Omland Fiskeadministrasjon. *Årbok 1975—76*: 42—54. (In Norwegian.)
- HANSEN, L. P. 1980 a. Merking av laksesmolt og laks på gytevandring i Vefsna og Vefsnfjorden. Direktoratet for Vilt- og Ferskvannsfisk. *Rapp. Fiskeforsk.* (6): 1—38. (In Norwegian.)
- 1980 b. Merking og utsetting av laksesmolt *Salmo salar* L. i Glomma. *Fauna* 33: 89—97. (In Norwegian with English summary.)
- ÍSAKSSON, Á. 1980. Salmon ranching in Iceland. p. 131—156. In *Salmon ranching*. Ed.: J. E. Thorpe. Academic Press Inc. Ltd., London.
- and P. K. BERGMAN. 1978. An evaluation of two tagging methods and survival rates of different age and treatment groups of hatchery-reared Atlantic salmon smolts. *J. Agr. Res. Icel.* 10(2): 74—99.
- JENSEN, K. W. 1979. Saltwater releases and saltwater adaption of smolts of Atlantic salmon. *ICES C.M.* 1979/M: 8. 10 p.
- JOHNSEN, B. O. 1978. Fiskeribiologiske undersøkelser i de lakseførende deler av Ranavassdraget. *DVF Reguleringsundersøkelsene i Nordland* (7): 1—54. (In Norwegian.)
- LARSSON, P.-O. 1980. Smolt rearing and the Baltic salmon fishery. p. 157—186. In *Salmon ranching*. Ed.: J. E. Thorpe. Academic Press, London.
- H.-O. LARSSON and C. ERIKSSON. 1979. Review of Swedish salmon (*Salmo salar* L.) stocks based on results of tagging experiments. *Rep. Swed. Salm. Res. Inst.* (5). 28 p. (In Swedish with English abstract.)
- NAEVDAL, G., Ø. BJERK, M. HOLM, R. LERØY and D. MØLLER. 1979. Growth rate and age at sexual maturity of Atlantic salmon smoltifying aged one and two years. *Fisk. Dir. Skr. HavUnders.* 17(1): 11—17.
- RITTER, J. A. 1975. Relationships of smolt size and age with age at first maturity in Atlantic salmon. Res. Dev. Branch. Environ., Can. Tech. Rep. Ser. No. Mar/F-75.5. 7 p.
- and T. G. CAREY. 1980. Salmon ranching in the Atlantic maritime provinces of Canada. p. 109—130. In *Salmon ranching*. Ed.: J. E. Thorpe. Academic Press, London.
- ROSSELAND, L. 1965. Merking av laksunger. *Årb. K. Norske Vidensk. Selsk. Museet, Trondheim*. p. 125—144. (In Norwegian.)
- 1969. Om virksomheten til Direktoratet for jakt, viltstell og ferskvannsfiske i 1968. *Landbruksdepartementet. St. meld.* 88. 70 p. (In Norwegian.)
- 1979. Erfaringer fra smoltutsettinger i regulerte vassdrag. p. 243—258. In *Vassdragsregulerings biologiske virkninger i magasiner og lakseelver*. Eds.: T. B. Gunnerød and P. Mellquist. Norges vassdrags- og elektrisitetsvesen. Direktoratet for vilt og ferskvannsfisk. (In Norwegian.)
- SAUNDERS, R. L. and K. R. ALLEN. 1967. Effects of tagging and fin-clipping on the survival and growth of Atlantic salmon between smolt and adult stages. *J. Fish. Res. Board Can.* 24(12): 2595—2611.
- THORPE, J. E. (Ed.). 1980. *Salmon ranching*. Academic Press, London. 441 p.

A Check on the Invertebrates of a Norwegian Hydroelectric Reservoir and Their Bearing Upon Fish Production

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ABSTRACT

The 36.7 km² Aursjøen reservoir has been regulated since 1953, and includes a main basin regulated 28 m and the Gautsjøen basin regulated 5 m. Brown trout (*Salmo trutta* L.) and grayling (*Thymallus thymallus* L.) are the only fishes present. The crustacean plankton seemed unaffected by the water fluctuations. The soft bottom and littoral fauna was dominated by Oligochaeta, Chironomidae, *Pisidium*, and the Cladocera *Eurycerus lamellatus*. Besides small numbers of Hydracarina and unidentified Diptera, 6 species of other insects, and 8 species of littoral Entomostraca were recorded. The material identified to the species level revealed only minor qualitative differences between the two basins. The biomass of benthos, mainly Chironomidae, in the Gautsjøen basin was several times higher than before regulation started. The basis of this high production of Chironomidae has to be the peat deposits of the impounded, boggy ground. Based on the biomass data and probable figures of the P/B relations, the estimated production of planktonic food organisms for fish exceeded the corresponding benthos with a factor of 140 for the main, and 5 for Gautsjøen basin. Stocking with a plankton-consuming fish, for example Arctic char, *Salvelinus alpinus* (L.), would probably tenfold the yield of fish.

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I. INTRODUCTION

The effects of the changed environment in the hydroelectric reservoirs upon the vegetation and fauna are known in broad outline. The consequences on fish production have drawn special attention. AXELSON (1961) and LÖTMARKER (1964) have studied crustacean plankton in reservoirs, and RODHE (1964) the fertilizing effect and blooming of plankton during the first years after impounding. The destructive effect of water level manipulations upon plants and invertebrates of the littoral has been described (STUBE 1958, HYNES 1961, GRIMÅS 1961 and 1962). None of these studies upon invertebrates have, however, been done in reservoirs regulated for more than 10—12 years.

The Aursjøen reservoir includes three lakes of different amplitude of water fluctuations over 25 years. Plans including increased impounding lead to this study, merely a check, upon the crustacean plankton and bottom animals. The results are, however, very unambiguous.

II. THE AURSJØEN RESERVOIR

The Aursjøen reservoir covers 36.7 km² and is 23 km long. It is located in the Dovrefjell area in Central Norway (Fig. 1).

Its catchment area consists of Pre-Eucambrian rocks, mainly folded granitic and granodiositic gneisses. The western part is mainly bedrock with scattered vegetation. Around the east end of the reservoir the terrain is flatter with some quaternary deposits, bogs and birch forest. Mountains ranging up to an altitude of 1,500—1,800 m surround the reservoir.

The annual precipitation is about 1,000 mm, much of which falls as snow. The average air temperature in July, the warmest month, does not exceed 13°C. The catchment area includes small glaciers, and large snowdrifts exist throughout the summer. The reservoir is exposed to strong western winds.

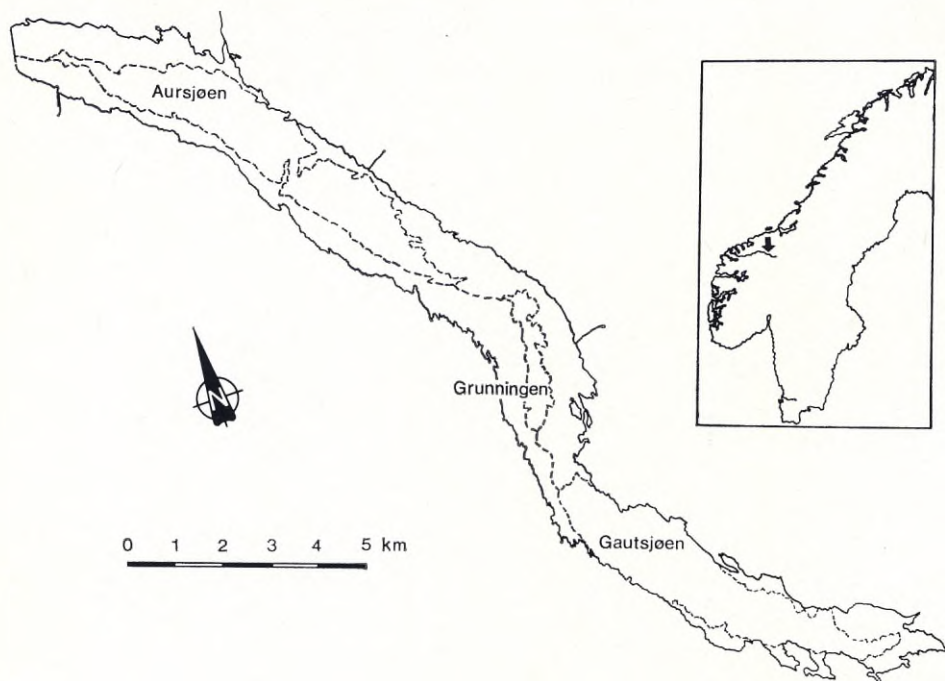


Fig. 1. Map of the Aursjøen reservoir and the original lakes.

The Aursjøen reservoir was made by damming the River Aura, and impounding the Lakes Aursjøen, Grunningen, and Gautsjøen to altitude 856 m (Fig. 1). The natural levels of the lakes were altitudes 831, 837.5, and 851 m, respectively. Now the lowest level of the Lake Aursjøen is 827.3 m, and the amplitude of water fluctuations is thus 28.7 m. When the reservoir is completely emptied, the Lake Gautsjøen will drain to altitude 843.5. This has happened only three or four times since the regulation started in 1953. During the last ten years the reservoir has most often been filled up in the autumn. The main basin, the former Lakes Aursjøen and Grunningen, has been drained about 20 m, to the natural level of the Lake Grunningen. The Gautsjøen basin has been lowered 5 m, to its original level.

The Aursjøen reservoir bears the impact of the water fluctuations. The impounded zone of the main reservoir consists of about 90 % naked bedrock and large stones, of which the former vegetation is washed out. The heavy erosion by wind and waves has washed the small particles and plant remains beneath the lowest water level.

Boulders and stones eroded by frost occur all over this zone.

The impounded zone of the Gautsjøen basin is much flatter and less eroded. About 50 % of this area is covered by black peat, and large stretches of gravel and sand exist. Fine particles and large amounts of peat are deposited on the former lake bottom.

The differences in levels of water fluctuation and substrate give rise to different ecosystems, which are also separated for most of the year.

III. MATERIAL AND METHODS

Water samples were taken with a Ruttner sampler at one station in the main reservoir and at one in the Gautsjøen reservoir.

Crustacean plankton were collected at 6 stations, mainly by vertical hauls from bottom to surface, at some stations also by a 25 l Schindler trap. The diameter of the net opening was 29 cm, the mesh size 90 μm . The quantitative samples were counted in total, and of the net hauls a fraction of 1/10.

Table 1. Mean number m^{-2} surface area of crustacean plankton, based on three vertical net hauls and net factor 2.

	Main reservoir		Gautsjöen reservoir	
	July 4	August 31	July 5	August 30
<i>Holopedium gibberum</i>	24,000	7,700	19,100	12,100
<i>Daphnia longispina</i>	6,300	7,200	100	0
<i>Bosmina longispina</i>	44,000	47,600	126,200	81,400
<i>Bythotrephes longimanus</i>	0	100	0	200
<i>Diaptomus</i> cop.	16,800	0	10,100	0
<i>Arctodiaptomus laticeps</i> ad.	0	18,600	0	10,900
<i>Mixodiaptomus laciniatus</i> ad.	0	0	0	200
<i>Heterocope saliens</i> cop.	21,300	0	8,200	0
<i>Heterocope saliens</i> ad.	0	2,700	0	9,200
<i>Cyclops scutifer</i> cop.	2,200	54,000	1,200	43,700
<i>Cyclops scutifer</i> ad.	15,000	800	6,600	0

Soft bottom animals were sampled by a Van Veen grab at different depths at 6 stations. In the impounded zone of the main reservoir it was very difficult to find any soft bottom. All grab samples contained much peat, from which it was very time-consuming to sort out the animals. Therefore each sample includes only two grabs, covering an area of 0.04 m^2 . The samples were sieved through a screen of mesh width 0.5 mm.

Littoral samples were taken at shallow water at 12 stations by a kicking technique described by FROST *et al.* (1971).

Strong wind and other problems made it impossible to sample all stations during the two periods of field work, July 4—5, and August 30—31, 1978. The water level of the main reservoir was altitude 848 in the first period and 849 in the second. Its surface area was 23 km^2 . The Gautsjöen reservoir remained in both periods at its original level, altitude 851, surface area 6.8 km^2 . The two basins had been separated since January—February.

IV. RESULTS

Hydrography

On July 4 the surface temperature in the main reservoir was 10.2°C. From 5 m depth to 20 m, near the bottom, the temperature fell from 9.7 to 6.7°C. The Gautsjöen reservoir was isothermal at 11°C. On August 31 the surface temperatures were 11.0°C in the main and 8.7°C in the Gautsjöen reservoir, falling to 10.4°C and 8.3°C near the bottom, at 30 and 15 m depth, respecti-

vely. The temperature of the main reservoir probably seldom exceeds 11°C. The smaller Gautsjöen reservoir is a little warmer, and cools down earlier in the autumn. The strong wind along the reservoir involves intense circulation and small vertical thermal and chemical differences. Electric conductivity 8—10 $\mu S/cm$, 0.3 mg/l CaO, Secchi depth 8.1 m and Secchi colour green show that the water quality is the typical of waters of the Norwegian mountains. A chloride content of 0.4—0.6 mg/l indicates that marine electrolytes, characterizing fresh water along the coast, do not reach the Aursjöen reservoir. pH values of 6.6—6.7 show that the acid precipitation enveloping Scandinavia from south (JENSEN and SNEKVIK 1972, WRIGHT and SNEKVIK 1978) does not yet touch this area.

Crustacean plankton

Eight species of crustacean plankton were recorded, 4 of Cladocera and 4 of Copepoda (Table 1). All of them are widespread in Scandinavia up to an altitude of 1,000 m, except *Mixodiaptomus laciniatus* (LILLJ.), the occurrence of which is more occasional south of the Arctic circle.

In the Schindler trap samples, the abundance of the different species in most cases was one individual l^{-1} . The most numerous species, *Holopedium gibberum* ZADDACH, *Bosmina longispina* LEYDIG, *Arctodiaptomus laticeps* (SARS), and *Heterocope saliens* (LILLJ.), occurred in many samples from the main reservoir in numbers of 2—5 l^{-1} . In the Gautsjöen reservoir this holds only

Table 2. Individual length (L) and weight (W), and dry weights m^{-2} of surface area of crustacean plankton August 31. In the equation $\ln W = \ln a + b \ln L$, a and b for *Holopedium gibberum* after LANGELAND (1982), for the other species after BOTTRELL *et al.* (1976).

	L mm	W μg	Main reservoir mg m^{-2}	Gautsjöen reservoir mg m^{-2}
<i>Holopedium gibberum</i>	1.16 ± 0.12	30	230	363
<i>Daphnia longispina</i>	1.68 ± 0.20	13	94	—
<i>Bosmina longispina</i>	0.63 ± 0.03	6	285	488
<i>Arctodiaptomus laticeps</i>	1.36 ± 0.05	7	130	76
<i>Heterocope saliens</i>	1.98 ± 0.07	27	73	248
<i>Cyclops scutifer</i>	0.45 ± 0.03	0.4	22	17
Cladocera			609	851
Copepoda			225	341
All crustacean plankton			834	1,192

for *B. longispina*, of which the maximum number here was 19 l^{-1} . The variations were large both vertically and from station to station. *H. gibberum* and *H. saliens* were, never-the-less, most numerous above 10 m depth. The concentration of all crustacean plankton varied from 0.3 to 20 l^{-1} . In 60 % of the samples the number was between 3 and 10.

To calculate the filtering efficiency of the plankton net, the number of individuals per m^2 surface area based on the samples of the Schindler trap were divided by the corresponding number of the vertical net hauls. For 8 vertical series the mean net factor varied from 1.3 to 2.3 for the different species, and for all crustaceans it was 1.9. Based upon these figures and corresponding results from comparable lakes, a net factor of 2.0 will be used in the further calculations.

The vertical net hauls also revealed large horizontal variations. Generally the numbers increased with increasing depth. Differences existed between the main reservoir and the Gautsjöen reservoir. *Daphnia longispina* (O. F. MÜLLER) occurred in small numbers in all samples of the main reservoir, but in the Gautsjöen reservoir only a few specimens were found in the east end on July 5. Both basins were then dominated by *B. longispina*. At the end of August copepodites of *Cyclops scutifer* SARS were most abundant in the main and *B. longispina* in the Gautsjöen reservoir.

The planktonic crustaceans seem to have traditional annual cycles in the Aursjøen reservoir. In the main reservoir *H. gibberum* was on the

decline at the end of August, while the abundance of *D. longispina* and *B. longispina* was similar to that of July. *A. laticeps* and *H. saliens* have, during the same period, metamorphosed from small copepodites to adults. Even *C. scutifer* shows an unusually clear cycle. On July 5 its populations held 85 % adults, which by August 31 had raised a new generation of copepodites and were dying.

The usual abundance of the different species was 10,000 to 30,000 individuals m^{-2} . *B. longispina* showed a maximum of 204,000 on July 5, and *C. scutifer* reached 89,000 individuals m^{-2} on August 31.

Based on the mean abundance of the vertical net hauls, the mean biomass of the crustacean plankton is calculated to 0.8 g m^{-2} for the main reservoir and 1.2 g m^{-2} for the Gautsjöen reservoir at the end of August (Table 2). The Cladocera represented about 70 %, and *H. gibberum* and *B. longispina* alone 50 % of the biomass.

The crustacean plankton biomass of Norwegian lakes in July—August is found to vary between 250 and $1,950 \text{ mg m}^{-2}$ when net factor 2 is used for vertical net hauls and mesh size $90 \mu\text{m}$ (LANGELAND 1972, 1974 a, 1974 b, 1975, 1978, REINERTSEN and LANGELAND 1978). Figures of $1,000 \text{ mg m}^{-2}$ are high, and for the Aursjøen reservoir they are probably partly a consequence of the negligible predation by the present fishes, brown trout (*Salmo trutta* L.) and grayling (*Thymallus thymallus* (L.)).

Table 3. Number of animals m^{-2} bottom area in grab samples.

Locality	Date	St.	Depth m	Oligochaeta	Ephemeroptera	Chironomidae	Hydracarina	Pisidium	Sum bottom dwellers	<i>Eurycercus lamellatus</i>
Main reservoir	July 4	1	3	200	—	20	—	—	220	30
			6	600	—	—	—	—	600	230
			12	—	—	100	—	—	100	450
			20	30	—	30	—	50	110	—
			22	30	—	100	—	130	—	
Main reservoir	August 31	2	1	150	—	30	—	—	180	30
			3	430	—	180	—	—	610	80
			5	450	—	400	—	100	950	150
			7	400	—	100	—	—	500	50
			10	200	—	400	—	50	650	—
			15	—	—	50	—	—	50	—
			20	80	—	80	—	160	—	
Main reservoir	August 31	3	3	100	—	100	—	—	200	50
			5	200	—	950	—	—	1,150	150
			12	100	—	—	—	—	100	250
Gautsjöen	July 5	5	1	530	—	30	—	—	560	—
			3	30	—	550	—	—	580	—
			5	—	30	500	—	—	530	—
			7	70	—	480	—	50	600	—
			10	—	—	80	—	50	130	—
Gautsjöen	July 5	6	1	480	—	—	—	180	660	—
			3	80	—	630	—	—	710	30
Gautsjöen	August 30	4	1	750	—	2,680	—	1,430	4,860	—
			3	430	—	1,600	—	900	2,930	50
			5	250	—	2,200	—	1,530	3,980	150
			7	100	—	950	—	450	1,500	100
			10	—	—	680	—	680	30	
Gautsjöen	August 30	5	1	230	—	950	20	—	1,200	80
			3	100	—	1,900	80	80	2,160	50
			5	150	—	1,230	—	—	1,380	—
			7	20	—	1,700	—	20	1,740	20
			10	70	—	1,590	—	—	1,660	150
Gautsjöen	August 30	6	1	880	—	2,330	—	50	3,260	—
			3	50	—	2,700	—	—	2,750	250
			5	230	—	1,930	—	—	2,160	100

Bottom animals

The grab samples contained no living plants. At one locality in the Gautsjöen reservoir some moss and a few specimens of *Callitriche polymorpha* LÖNNR. were observed.

The results of the grab samples are given in Table 3 and Fig. 2. The soft bottom fauna was almost completely composed of four groups, Oligochaeta, Chironomidae, *Pisidium* and one

species of Cladocera, *Eurycercus lamellatus* (O. F. MÜLLER). Besides, one larva of Ephemeroptera and four individuals of Hydracarina were recorded. Oligochaeta and Chironomidae were dominant, and often the only animals present.

In the main reservoir the maximum number of bottom animals on July 4 was found at 6 m depth, 600 individuals m^{-2} , with a wet weight of 2.33 g, *E. lamellatus* not taken into account. At the other

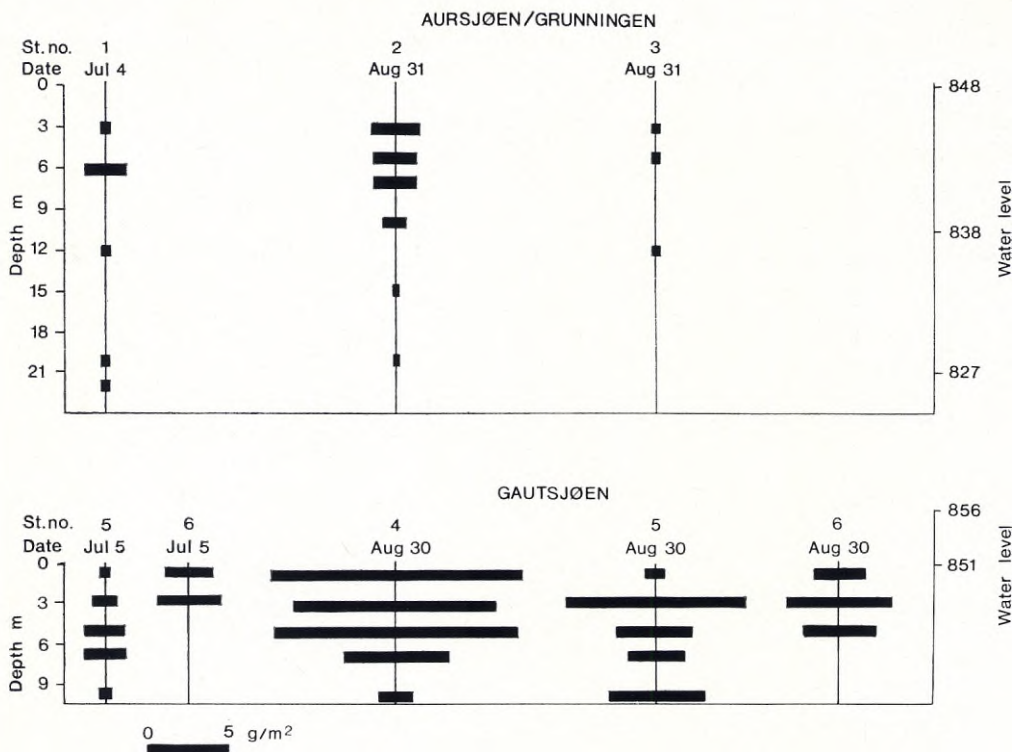


Fig. 2. The vertical distribution of soft bottom animals in the Aursjøen main reservoir and the Gautsjøen reservoir.

depths the numbers varied between 110 and 230, and the biomass between 0.28 and 2.67 g. On August 31 the variation in the depth zone 3 to 7 m at St. 2 was from 500 individuals and 2.44 g to 950 individuals and 2.93 g per m^2 . At St. 3 and always below 10 m depth the biomass of bottom animals was less than $0.8 g m^{-2}$.

In the Gautsjøen reservoir no grab samples were taken deeper than 10 m. The total numbers

m^{-2} on July 5 were mainly 500–600. On August 30 the abundance of Chironomidae had increased, and varied between 680 and 2,680 m^{-2} . *Pisidium* occurred more patchily, but reached 1,530 individuals and $9.39 g m^{-2}$. The total number of bottom animals was maximum 4,860 individuals and $15.50 g m^{-2}$, and the mean figures 2,330 individuals and $7.10 g m^{-2}$.

The soft bottom fauna of the three intact lakes

Table 4. Number and wet weight (g) of soft bottom animals m^{-2} in the Lakes Gautsjøen, Grunningen, and Aursjøen before impounding, and in the Aursjøen reservoir 1978. *Eurycercus lamellatus* is excluded from the 1978 material.

		Mean < 12 m depth		Maximum		Minimum	
		No	g	No	g	No	g
1950–1953	Intact lakes	470	3.1	753	4.7	251	0.7
July 1978	Main reservoir	410	1.4	600	2.3	100	0.1
August 1978	Main reservoir	610	1.5	950	3.0	50	0.1
July 1978	Gautsjøen reservoir	540	2.1	710	3.9	130	0.6
August 1978	Gautsjøen reservoir	2,330	7.1	4,860	15.5	680	1.2

Table 5. Biomass m^{-2} of bottom animals in some Norwegian reservoirs.

Locality	Date	Regulated		Impounded	Wet weight $g\ m^{-2}$			Reference
		No. years	m	m	1—5 m	6—10 m	10 m	
Finnkojsjön	July 14	1	6	6	1)	10.3	8.7	JENSEN 1973
Gautsjöen	August 30	25	5	5	8.2	4.6	—	
Selbusjön	July 2	54	6	—	1.2	9.0	0.3	LANGELAND 1976
Selbusjön	August 22	54	6	—	3.2	6.0	0.3	LANGELAND 1976
Gautsjöen	July 5	25	5	5	2.3	1.6	—	
Aursjön, main reservoir	August 31	25	29	25	1.4	1.9	0.3	
Aursjön, main reservoir	July 4	25	29	25	0.4	2.4	0.4	
Holden	July 15	60	10	12	1.1	0.7	0.5	JENSEN 1972
Storvatn	July 10	13	6	—	1.0	0.5	0.3	LANGELAND 1974 b
Gjølgevatn	June 10	12	4	—	1.0	0.5	—	JENSEN (unpubl.)
Samsjön	July	41	11	—	0.6	0.8	0.4	SIVERTSEN, E. (pers. com.)

1) Grabbing impossible.

was investigated in 1950—53, before impounding and regulation. The results have not been properly published, but ÖKLAND (1963) gives some information, which in Table 4 is compared with the figures of 1978. The mean values of 1978 are less reliable, but the maximum values favour the 1950—53 results, since the grabbing programme then was far more extensive. In July the abundance both in the main reservoir and the Gautsjöen reservoir was of the same order as before impounding, but the biomass was smaller. The larger animals, such as *Gammarus*, Gastropoda, larvae of Ephemeroptera, Plecoptera, and Trichoptera, had disappeared and been replaced mainly by Oligochaeta and Chironomidae of less individual weight. In late summer the situation was much the same in the main reservoir, but in the Gautsjöen reservoir the abundance was 5—6 times and the biomass 2—3 times larger than in the intact lakes. This is mainly due to increased numbers of Chironomidae and more occasionally of *Pisidium*. According to ÖKLAND (1963) the Gautsjöen reservoir has both a larger abundance and biomass of soft bottom animals than most Norwegian lakes.

Table 5 reviews the wet weights of soft bottom animals in some Norwegian hydroelectric reservoirs. The Aursjön main reservoir represents a typical case with small weights all over. The Gautsjöen reservoir is only surpassed by the

Finnkojsjö reservoir, where the biomass in the same way increased after impounding by the advance of Chironomidae (JENSEN 1973). LANGELAND (1976) also found comparable weights of Chironomidae on patches covered with organic matter in the Selbusjön reservoir.

The mean individual wet weight of Oligochaeta increased from 3.3 to 5.4 mg, and decreased for *Pisidium* from 5.9 to 5.1 mg during the summer. For Chironomidae it was divided in half, from 4.0 to 2.0, while their number increased several times in the Gautsjöen reservoir. Consequently, new generations of Chironomidae have been born, and the bulk must hatch immediately after the breaking up of the ice.

The kick samples at two stations gave a total of 140—150 individuals, elsewhere the numbers were 8—80 (Table 6). Oligochaeta occurred on every station but one. Two species of Cladocera, *E. lamellatus* and *Sida crystallina* (O. F. MÜLLER), were normally dominating in number, especially in late August. Otherwise, only fragments of the littoral fauna of an intact lake were found: of Ephemeroptera some specimens of *Siphonurus lacustris* ETN. and one *Baëtis rhodani* (PICT.), of Plecoptera one *Diura bicaudata* (L.), of Trichoptera one *Apatania* sp. and one Limnephilidae. The Coleoptera *Deronectes alpinus* PAYK. was present on several stations in the Gautsjöen reservoir. The complete sampling programme gave one to five

Table 6. Number of animals in 5 minutes kick samples.

Date	Main reservoir							Gautsjöen reservoir					
	July 4			August 31				July 5			August 30		
Oligochaeta	5	63	8	4	14	5	3	16	—	122	5	16	12
Cladocera													
<i>Eurycerus lamellatus</i>	2	—	—	—	75	20	—	—	22	5	49	1	18
<i>Sida crystallina</i>	9	—	—	38	27	—	—	—	2	—	2	—	—
Ephemeroptera													
<i>Siphonurus lacustris</i>	—	—	1	—	1	—	—	—	—	20	1	—	2
Plecoptera													
<i>Diura bicaudata</i>	—	—	—	—	—	—	—	—	—	—	—	1	—
Trichoptera													
<i>Apatania</i> sp.	—	—	—	—	1	—	—	—	—	—	—	—	—
Limnephilidae	—	—	—	—	—	—	—	—	—	—	—	1	—
Chironomidae	—	—	—	—	2	—	5	—	—	—	5	1	—
Other Diptera	—	5	—	1	21	—	—	—	—	—	1	6	4
Hydradephaga													
<i>Deronectes alpinus</i>	—	—	—	—	—	—	—	2	—	5	—	2	4
Hydracarina	—	2	—	—	—	1	—	—	—	—	—	—	—
<i>Pisidium</i>	—	10	—	—	5	—	—	—	—	—	1	—	—
Sum	16	80	9	43	146	26	8	18	24	152	64	28	40

individuals of the following littoral Cladocera: *Ophryoxus gracilis* Sars, *Acroperus harpae* Baird, *Alona affinis* Leydig, and *Chydorus* sp. A few copepodites, stages IV and V, of the littoral Copepoda *Acanthocyclops* and *Eucyclops* were also found.

Comments upon biomass and production

The reflections on biomass are based upon the following assumptions. The actual productive area of the main reservoir was 23 km² and of the Gautsjöen reservoir 6.8 km². Naked, unproductive bedrock is supposed to cover 90 % of the impounded area above and 30 % below level 838 m of the main reservoir. The dry weight of bottom animals make up 10 % of the wet weight (DAHL 1930, AAGAARD 1978). Nauplii of Copepoda, the small populations of *B. longimanus* and *M. laciniatus* as well as the poor littoral fauna above 1 m depth are disregarded. For comparison the August values are chosen, when the biomass of crustacean plankton was smallest and that of bottom animals largest.

Even though the statistical significance of the figures is low, it is evident that the biomass of bottom animals is only a small fraction of that of the crustacean plankton in the main reservoir (Table 7). For the Gautsjöen reservoir the estimates

give a proportion of 1:3, in spite of the high abundance of bottom animals. Relations between crustacean plankton and bottom animals corresponding to the last figures are reported by DAHL (1930) from several Norwegian lakes.

The estimates of production are based upon the following assumptions. Between the annual production and mean biomass of the growth season (P/B), the following relations are found for different fauna groups: planktonic Cladocera 10 in lakes where the temperature reach 14–15°C, and about 2 per month at temperatures of 10–11°C (WINBERG *et al.* 1971, LANGELAND 1982), planktonic Copepoda 2–4 (LANGELAND 1982, JENSEN 1980), *Pisidium* and Chironomidae 0.8–2.2 decreasing with the life span (WINBERG *et al.* 1971, Aagaard 1978). For further calculations on the Aursjöen reservoir a P/B coefficient of 4 is chosen for Cladocera and 2 for Copepoda and bottom animals. Based on the biomass estimates of August, this will lead to a production underestimate of the crustacean plankton and an overestimate of the bottom animals.

On these premises the production of crustacean plankton and bottom animals of the main reservoir were respectively 66,600 and 1,100 kg dry weight (Table 7). The corresponding figures for the Gautsjöen reservoir were 27,800 and 6,400 kg.

Table 7. Estimates of standing biomass Aug 31 and annual production of different groups of invertebrates in the Aursjoen reservoir, kg dry weight.

	Main reservoir		Gautsjoen reservoir	
	Biomass	Production	Biomass	Production
Cladocera	14,000	56,000	5,800	23,200
Copepoda	5,300	10,600	2,300	4,600
Sum crustacean plankton	19,300	66,600	8,100	27,800
<i>Eurycercus</i> , Chironomidae, and <i>Pisidium</i>	200	400	2,400	4,800
Other bottom animals	350	700	800	1,600
Sum bottom animals	550	1,100	3,200	6,400

V. DISCUSSION

Four species of planktonic Cladocera and three of Copepoda were found in the Aursjoen main reservoir. This number is equal to the mean number of 13 lakes of northern Sweden (LOTMARKER 1964), and larger than the number PENNAK (1957) finds typical of lakes on a global scale. The biomass of crustacean plankton was large compared with other Norwegian lakes, but the predation by fishes is small. The crustacean plankton seems unaffected by the water fluctuations. This is in accordance with the conclusions of AXELSSON (1961) and LOTMARKER (1964) for Swedish reservoirs.

The abundance of the littoral Cladocera *Eurycercus lamellatus* was fairly high down to 10 m depth, and some *Sida crystallina* occurred above 1 m depth. In addition, four species of littoral Cladocera and two of Copepoda were recorded in numbers from one to five.

The bottom fauna was mainly composed of Oligochaeta, Chironomidae and *Pisidium*. Besides Diptera, only 6 species of insects were recorded, and of them *Siphonurus lacustris* seems to best tolerate the water fluctuations. The rest fauna of the groups Ephemeroptera, Plecoptera, and Trichoptera included 5 species, compared with 13 in the Blasjoen reservoir in Sweden after 6 m regulation over 9 years (GRIMAS 1961 and 1962). The sampling in the Blasjoen reservoir was much more intensive, but the main reservoir of Aursjoen has, on the other hand, been exposed to a higher amplitude of water fluctuation over a longer period. The qualitative damage on the bottom fauna is probably worse than in other Scandinavian reservoirs investigated.

In the Gautsjoen basin one additional species of planktonic Copepoda and one of bottom animals, the Coleoptera *Deronectes alpinus*, were found. The abundance and biomass of the benthic fauna, and especially of the Chironomidae, in the Gautsjoen reservoir was on the contrary much higher than before regulation started. The corresponding situation is known from the Finnkojsjoen reservoir (JENSEN 1973). In the Nesjo reservoir the stomachs of the brown trout and Arctic char are stuffed with Chironomidae the first month after the breaking up of the ice (JENSEN 1979 a and 1979 b). Common for these reservoirs are large areas of impounded, flat bogs, where the peat partly lies intact and partly is spread out over the reservoir bottom. The base for the high production of Chironomidae has to be that peat. The bottom fauna of such reservoirs has much in common with the profundal fauna of eutrophic lakes, the peat being the storage of organic matter, providing a high production of specialized species. The production will gradually decrease as the plant remains will decompose or are covered with sediments. Based on the situation in many reservoirs, including the Holden reservoir of Northern Trondelag impounded 70 years ago (JENSEN 1972), the decomposition is very slow. The speed of sedimentation will especially depend upon the quality and extent of quaternary deposits around the reservoir and the degree of wave action. From the situation in the Gautsjoen reservoir, one would predict that a high production of these specialized bottom animals will be maintained for a 100 years, and probably longer. This longterm positive effect must be distinguished from the bloom of Cladocera

during the first few years after the impounding of lakes.

According to AASS (1969) Crustacea was the most important food item of brown trout in the Aursjøen reservoir during August–September 1965–68, supplemented by terrestrial insects, Chironomidae and some Tipulidae and Plecoptera. The crustaceans were mainly *E. lamellatus*, *Lepidurus arcticus* PALLAS, and *B. longimanus*, but also some *Daphnia* and *H. gibberum*. The grayling had specialized on *E. lamellatus*. Such a food consumption is quite in accordance with the available food fauna described by this survey, except that *L. arcticus* was not recorded. AASS (1969) states that *L. arcticus* has colonized the Aursjøen reservoir after the impounding. Its abundance is unclear.

The presented estimates on production favour in all steps the benthos in relation to the crustacean plankton. Considering only the animals eaten by the brown trout and the grayling, the production of planktonic Cladocera is of the order 140 times larger than of *Eurycercus*, Chironomidae, and *Pisidium* in the main reservoir, and 5 times in the Gautsjøen reservoir. In oligotrophic lakes plankton-feeding fishes can consume as much as 75 % of net zooplankton production, and the production of such fishes makes up about 10 % of the zooplankton production (HILLBRICHT-ILKOWSKA 1977). This production ratio seems to have general ecological value, and can also be accepted for fish-benthos. Intensive predation by fishes will lower the standing biomass of prey. But it is also known to cause an increase of the P/B ratio of zooplankton (HILLBRICHT-ILKOWSKA *op. cit.*). Assuming a water content of 75 % in fish (A. J. JENSEN 1979) and a harvest of 25 % of the yearly fish production, the potential fish yield (wet weight) is 0.1 of the production of prey animals (Table 7). Thus the potential fish yield of the main reservoir based on benthos is less than a 100 kg, while the planktonic Cladocera should provide more than 5,000 kg. The corresponding figures of the Gautsjøen reservoir are roughly 500 kg compared to 2,300 kg. The water height of 1978 considered, this represents 2.5 kg ha⁻¹ for the main and 4.1 for the Gautsjøen reservoir, figures which are within the accepted levels of Scandinavian reservoirs. The actual fish production of the Aursjøen reservoir is probably

only 10 % of the potential, which depends on the absence of a plankton-consuming fish. Fishing with standard series of bottom nets has thus revealed that reservoirs stocked with Arctic char, *Salvelinus alpinus* (L.), yield three to five times more than those stocked exclusively with brown trout (JENSEN 1979 a). The best fishing of brown trout and Arctic char ever reported from Norway (JENSEN 1979 a and 1979 b) takes place in the Nesjøen reservoir, located at altitude 720 m in the county of Sør-Trøndelag. Its invertebrate fauna is very much similar to that of the Gautsjøen reservoir. Arctic char make up about 90 % of the catches. The main food is planktonic Cladocera, but the key to the success is the Chironomidae, hatching from the breaking up of the ice to mid-July. The Chironomidae fill the gap in food access during the first month of the growth season, which exists in most reservoirs until the populations of *Eurycercus* and planktonic Cladocera are dense enough for fish predation.

Stocked with planktonic-feeding fishes, such as Arctic char or whitefish, *Coregonus lavaretus* (L.), the fish production of reservoirs like the main basin of Aursjøen is probably not reduced by more than 20 % compared to the unregulated state. Reservoirs of the Gautsjøen type will on the same premises for many, say 100, years produce more fish than the intact lake.

Hitherto, the official management of reservoirs in Norway has consisted of attempts to keep up the fishing of brown trout (AASS 1969). This is accompanied by expensive stockings, because the recruitment of brown trout is small in most reservoirs. The Arctic char, on the contrary, has a high potential of recruitment, and 'overpopulation' is often a problem. The char seems, however, to be easier to handle in reservoirs than in intact lakes, probably as a result of reduced spawning facilities. At least the yield of Arctic char is larger in reservoirs than in comparable intact lakes of Mid-Norway (JENSEN 1979 a).

A proper management of reservoirs should concentrate on Arctic char, which can compete with the brown trout in every respect as a fish for consumption. In Norway several reservoirs of the Gautsjøen type are under construction, some of them covering larger areas of wetland.

They should be stocked with Arctic char from the start. At present the right to fish with nets and other effective tackle is usually granted to only a few persons. They are by no means able to catch the quantity necessary to avoid overpopulation, nor the potential yields. The most important and greatest task in the management of Norwegian lakes and reservoirs, is to provide access to fishing with effective tackle on a much larger scale.

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VII. REFERENCES

- AAGAARD, K. 1978. The chironomids of Lake Målsjøen. A phenological, diversity, and production study. *Norw. J. Ent.* 25: 21—37.
- AASS, P. 1969. Crustacea, especially *Lepidurus arcticus* PALLAS, as brown trout food in Norwegian mountain reservoirs. *Rep. Inst. Freshw. Res., Drottningholm* 49: 183—201.
- AXELSON, J. 1961. Zooplankton and impounding of two lakes in Northern Sweden. *Rep. Inst. Freshw. Res., Drottningholm* 42: 84—168.
- BOTTRELL, H. H., A. DUNCAN, Z. M. GLIWICS, E. GRYGIEREK, A. HERZIG, A. HILLBRICHT-ILKOWSKA, H. KURASAWA, P. LARSSON and T. WĘGLENSKA. 1976. A review of some problems in zooplankton production studies. *Norweg. J. Zool.* 24: 419—456.
- DAHL, K. 1930. A study on the supplies of fish food organisms in Norwegian lakes. *Skr. norske Vidensk.-Akad. Mat.-naturv. Kl.* (1): 1—58.
- FROST, S., A. HUNI and W. E. KERSHAW. 1971. Evaluation of a kicking technique for sampling stream bottom fauna. *Can. J. Zool.* 49: 167—173.
- GRIMÅS, U. 1961. The bottom fauna of natural and impounded lakes in northern Sweden (Ankarvattnet and Blåsjön). *Rep. Inst. Freshw. Res., Drottningholm* 42: 183—237.
- 1962. The effect of increased water level fluctuation upon the bottom fauna in Lake Blåsjön, northern Sweden. *Rep. Inst. Freshw. Res., Drottningholm* 44: 14—41.
- HILLBRICHT-ILKOWSKA, A. 1977. Trophic relations and energy flow in pelagic plankton. *Pol. ecol. Stud.* 3(1): 3—98.
- HYNES, H. B. N. 1961. The effect of water-level fluctuations on littoral fauna. *Verh. internat. Ver. Limnol.* 14: 652—656.
- JENSEN, A. J. 1979. Energy content analysis from weight and liver index measurements of immature pollock (*Pollachinus virens*). *J. Fish. Res. Board Can.* 36(10): 1207—1213.
- JENSEN, J. W. 1972. Fisket i et kraftverksmagasin etter 60 års regulering (Holden, Verran). *K. norske Vidensk. Selsk. Mus., LFI-rapp.* 12: 1—31. (In Norwegian.)
- 1973. Fiskeribiologiske undersøkelser i Gammelvoldsjø og Finnkojsjø 1971. *K. norske Vidensk. Selsk. Mus., LFI-rapp.* 15: 1—29. (In Norwegian.)
- 1979 a. Variation in catches on standard series of bottom nets in Norwegian trout and char lakes. In The use of ecological variables in environmental monitoring. *The National Swedish Environment Protection Board, Rep. PM 1151: 212—219.*
- 1979 b. Fisken og fisket etter oppdemninger i Nea. In Vassdragsregulerings biologiske virkninger i magasiner og lakselver. Eds.: T. B. Gunnerød and P. Mellquist. NVE/DVF-symposium 29.—31. mai 1978: 85—92. (In Norwegian.)
- 1980. The annual cycle and production of *Arctodiaptomus laticeps* (SARS) in Lake Målsjøen, Norway. *J. Plankton Res.* 3: 283—289.
- JENSEN, K. W. and E. SNEKVIK. 1972. Low pH levels wipe out salmon and trout populations in southernmost Norway. *Ambio* 1: 223—225.
- LANGELAND, A. 1972. A comparison of the zooplankton communities in seven mountain lakes near Lillehammer, Norway (1896 and 1981). *Norweg. J. Zool.* 20: 213—226.
- 1974 a. Ørretbestanden i Holden i Nord-Trøndelag, etter 60 års regulering. *K. norske Vidensk. Selsk. Mus. Rapp. Zool. Ser.* 10: 1—21. (In Norwegian.)
- 1974 b. Virkninger på fiskebestand og næringsdyr av regulering og utrasing i Storvatnet i Rissa og Leksvik kommuner. *K. norske Vidensk. Selsk. Mus. Rapp. Zool. Ser.* 2: 1—20. (In Norwegian.)
- 1975. Virkninger på fiskeribiologiske forhold i Tunnsjøflyene etter 11 års regulering. *K. norske Vidensk. Selsk. Mus. Rapp. Zool. Ser.* 16: 1—27. (In Norwegian.)
- 1976. Fiskeribiologiske undersøkelser i Selbusjøen 1973—75. *K. norske Vidensk. Selsk. Mus. Rapp. Zool. Ser.* 5: 1—73. (In Norwegian.)
- 1978. Fiskeribiologiske undersøkelser i vatn i Sandölavassdraget, Nord-Trøndelag, somrene 1976 og 1977. *K. norske Vidensk. Selsk. Mus. Rapp. Zool. Ser.* 5: 1—27. (In Norwegian.)
- 1982. Interaction between zooplankton and fish in a fertilized lake. *Holarct. Ecol.* 5: 273—310.
- LÖTMARKER, T. 1964. Studies on planctonic Crustacea in thirteen lakes in Northern Sweden. *Rep. Inst. Freshw. Res., Drottningholm* 45: 113—176.
- PENNAK, R. W. 1957. Species composition of limnetic zooplankton communities. *Limnol. Oceanogr.* 2: 222—232.
- REINERTSEN, H. and A. LANGELAND. 1978. Vurderinger av kjemiske og biologiske forhold i Neavassdraget. *K. norske Vidensk. Selsk. Mus. Rapp. Zool. Ser.* 2: 1—55. (In Norwegian.)

- RHODE, W. 1964. Effects of impoundment on water chemistry and plankton in Lake Ransaren (Swedish Lappland). *Verh. Internat. Verein. Limnol.* 15: 437—443.
- STUBE, M 1958. The fauna of a regulated lake. *Rep. Inst. Freshw. Res., Drottningholm* 39: 162—224.
- WINBERG, G. G., K. PATALAS, J. C. WRIGHT, A. HILLBRICHT-ILKOWSKA, W. E. COPPER and K. H. MANN. 1971. Methods for calculating productivity. In *A manual on methods for the assessment of secondary productivity in fresh waters*. Eds.: W. T. Edmondson and G. G. Winberg. *IBP Handbook* 17: 296—317.
- WRIGHT, R. F. and E. SNEKVIK. 1978. Acid precipitation: chemistry and fish populations in 800 lakes in southernmost Norway. *Verh. Internat. Verein. Limnol.* 20: 765—775.
- ØKLAND, J. 1963. A review of the quantity of bottom fauna in Norwegian lakes and rivers. *Fauna, Oslo*, 16 (*Suppl.*): 1—67.

Adaptive Differences in the Long-Distance Migration of Some Trout (*Salmo trutta* L.) Stocks

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ABSTRACT

Tagging operations revealed the movements of four stocks of trout (*Salmo trutta* L.) in various Baltic Sea environments to which they were transported. The Dalälven stock proved to be coastal, with some incidence of straggling non-homing specimens. The Gullspång trout roamed about widely in open water, except in the cold Bothnian Bay, and had strong correlated homing behaviour. The downstream Verke trout had a NE-directed trend of movement and perfect homing. The upstream Verke trout is resident above waterfalls and did not migrate when transplanted. Evidence is presented for adaptation by natural selection in all cases. Selection for or against homing during repeated glacial periods is briefly discussed.

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I. INTRODUCTION

RICKER (1972) wrote an extensive review of the worldwide work, done mainly on *Oncorhynchus* and *Salmo*, in order to determine the environmental or genetic basis of various morphological and ecological stock traits. In most cases the analysis could prove the existence of a core of hereditary origin masked by a greater amount of phenotypic modification.

WADDINGTON (1942, 1953, 1957) provided an explanation of the evolutionary mechanism involved, based on his *Drosophila* studies. Ontogenetic development may be more or less strongly modified by the local environment (e.g. temperature) and, especially in extreme habitats, a canalizing selection creates a genetic assimilation of part

of the effect produced by the environment. A similar type of genetic assimilation may occur in traits such as growth, sexual maturity or migrational patterns.

Allelic frequency studies of proteins have lately been used as a standard method of proving overall genetic differences between stocks of the same fish species. Unfortunately, however, organismal and molecular evolution are out of step (CLAYTON 1981). Natural selection is the predominating force driving organismal evolution, while the 'molecular clock', migration and genetic drift are supposed to cause molecular evolution. It follows that electrophoretic techniques cannot be used to prove to what extent a certain stock trait, important in fisheries management, is in fact genetically based and thus comparatively stable.

LARSSON *et al.* (1979) summarized the yields of trout (*Salmo trutta*) taggings in the Baltic, based on 15,600 recoveries from 29 different stocks of trout. Five of these were consistently the best producers. Different migrational patterns have long been thought to occur in trout and STEFFNER (1975) proved that there was more dispersal among Gullspång trout than Dalälven trout, when both stocks were released in the Bråviken bay area.

The purpose of the present paper is to penetrate somewhat deeper into these migrational patterns in trout and their adaptive nature.

II. MATERIAL AND METHODS

Brown trout, artificially raised and released into Swedish fresh waters, as two-year olds, produced poor returns for commercial as well as sport fisheries (SVÄRDSON and NILSSON 1965). In the brackish Baltic Sea, however, results were better, though not as good as those obtained by releasing tagged natural smolts (SVÄRDSON and ANHEDEN 1963 a).

Stimulated by the better yields in the Baltic, various authorities funded an extensive series of trout stockings in the 1960's and 1970's. Many different stocks were used, according to what was available and thought to be a good choice.

A better planned test of the performance of trout stocks was started by the Institute of Freshwater Research in 1959, based on the Kälärne and Älvkarleby hatcheries. Other authorities later participated in the test by using the same stocks.

The trout were marked with Carlin tags. These served well, though designed for Atlantic salmon. In some cases tag losses were significant (SVÄRDSON and ANHEDEN 1963 a). There is evidence of slightly slower growth and higher mortality in tagged fish, compared to untagged fish.

Except for the natural smolts of the Verke river (also introduced to the Nybro river) all trout were first generation hatchery smolts, two years of age and released in early summer. The eggs, taken from the river, may in some cases (Gullspång and Dalälven stocks) have originated from fish which were themselves reared in hatcheries before their sea sojourn.

The transport of smolts is a stressful process which influences their survival. For obvious rea-

sons some transports had to be longer than others. Economic and other aspects interfered with and modified the program. The Älvkarleby hatchery was responsible for the production of about half of the smolts dealt with in this paper.

Due to practical considerations, the trout could not be released along the coast at those points where maximum information about dispersal could be obtained. It was also necessary to take care not to genetically contaminate some important local stocks, e.g., those of the Rivers Em and Mörrum.

The Gullspång trout is native to Lake Vänern. The Dalälven trout is one of the most widely used Baltic stocks, since both the Älvkarleby hatchery and the Salmon Research Institute are situated on the river. The Verke river, in the province of Skåne (Scania), for many years had a commercial weir for trout at its mouth, prompting various studies on its trout population.

III. RESULTS

Verke river trout, natural smolts

The Verke river runs from the southeastern part of the province of Skåne east to the Hanö bay, about 20 km north of the town of Simrishamn. Its width is 6—10 metres. There are no rapids, but ten km from the river mouth, some steep waterfalls block the further upstream movement of sea-running trout. Above the falls there is a resident, non-migratory trout stock (SVÄRDSON and ANHEDEN 1963 b).

The emigration of smolt, studied in a downstream weir for five years, takes place between May 3 and June 6 (SVÄRDSON 1966), although a

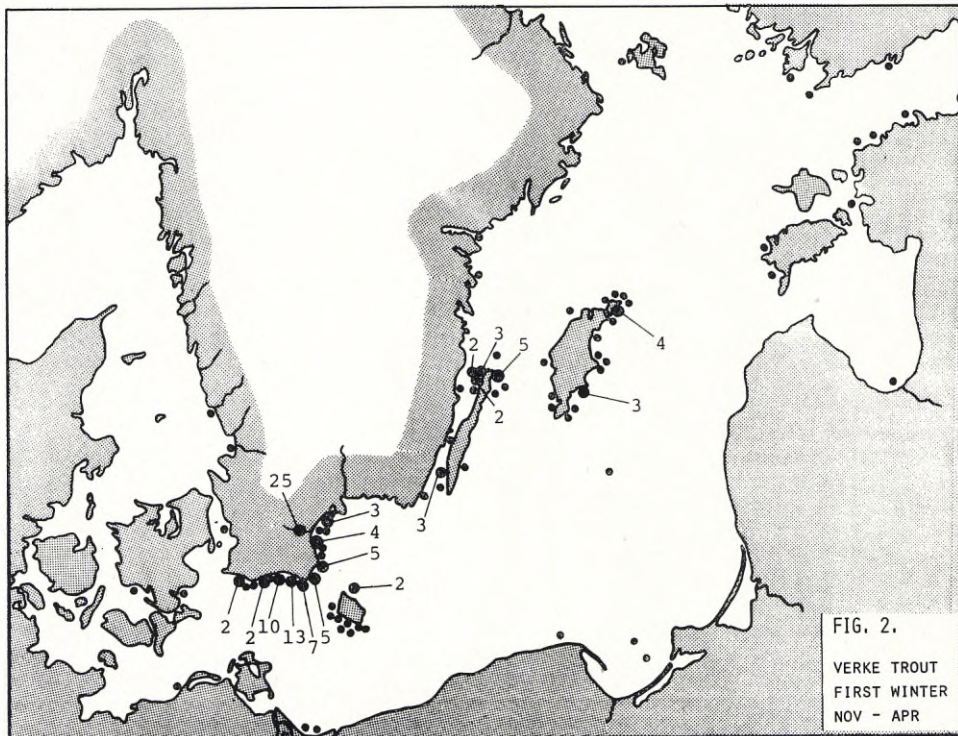
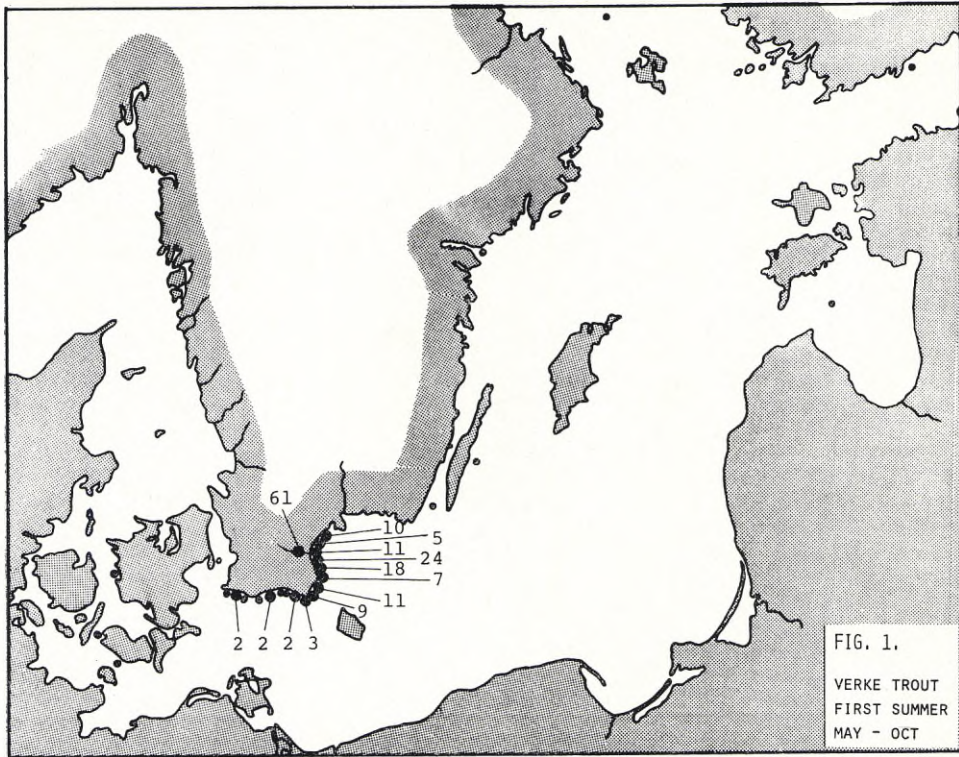
Recovered tagged trout are shown by dots. A small dot represents a single find. Larger dots represent several trout found in the same locality, and the accompanying figure indicates how many specimens were caught there. A figure surrounded by a circle shows the number of tags reported by Danish fishermen from the "southern Baltic". The details of every experiment are given in the figures, including the type of stock, the date and locality of release and the numbers of tagged and recovered trout.

Figs. 1—7 reveal the movements of the natural Verke river smolts during half-year periods. Fig. 8 shows the dispersal of natural smolts from the Nybro river, to which the Verke stock has been transplanted.

Figs. 9—15. The dispersal of hatchery smolts of the Verke stock, raised and released in various places. Fig. 15 shows the migration of Verke smolts from the Älvkarleby hatchery, released in the Verke river mouth, to be the same as that of natural smolts.

Figs. 16—24. The movements of hatchery smolts of the Gullspång stock, released in different localities, including Lake Vänern, their home lake.

Figs. 25—37. The movements of hatchery smolts of the Dalälven stock, released in different localities, including their home river.



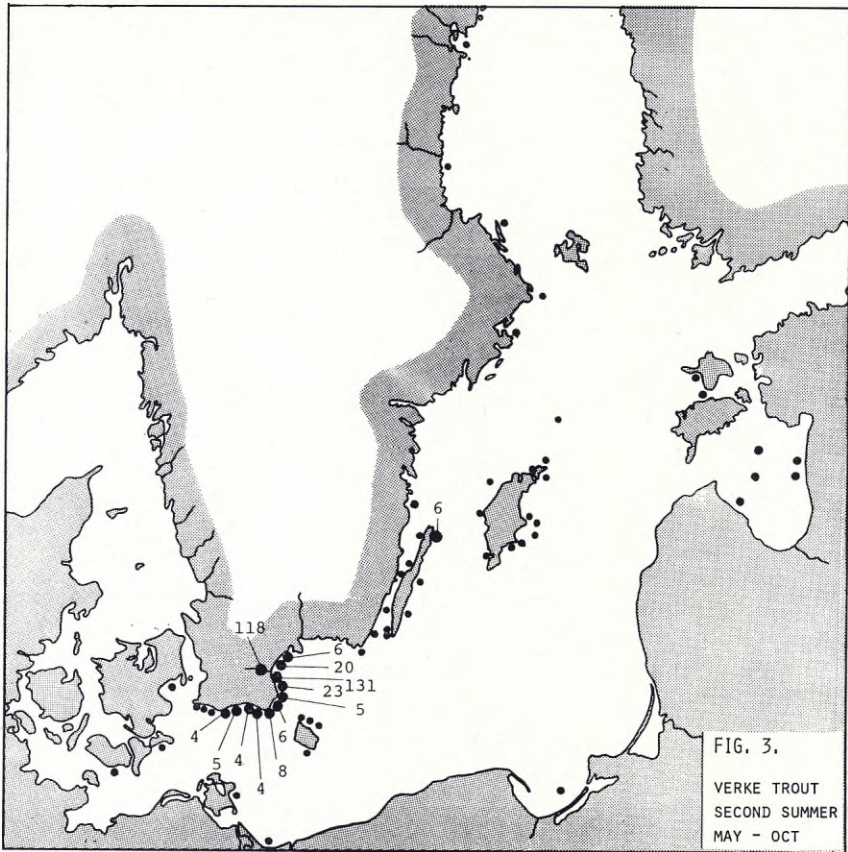


FIG. 3.
VERKE TROUT
SECOND SUMMER
MAY - OCT

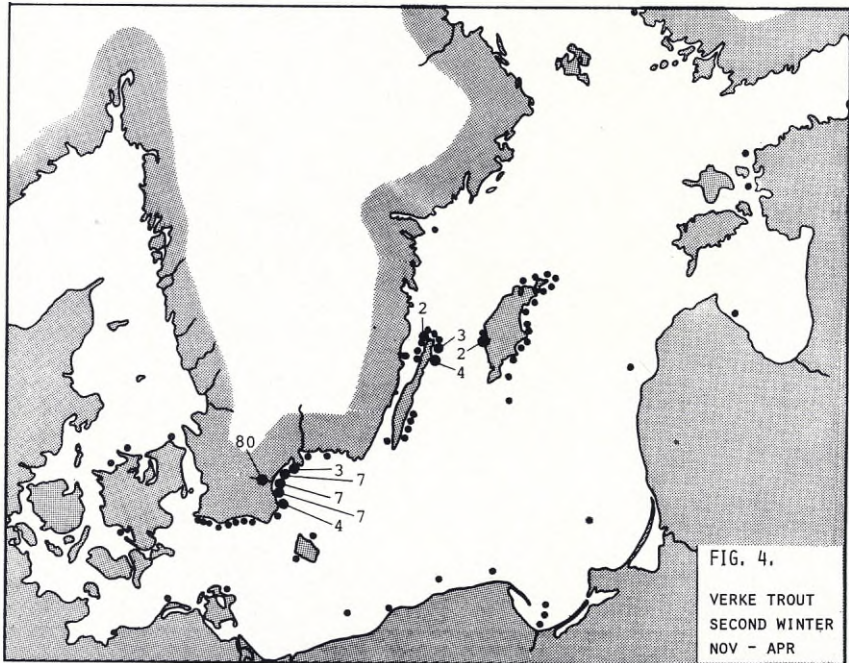


FIG. 4.
VERKE TROUT
SECOND WINTER
NOV - APR

few may already run in the last days of March or during April, and some late specimens appear through June until the first week of July. Three-year olds are few in number and start the run. No one-year-old smolts were found. The smolt are 14—19 cm in total length.

Samples of smolt, taken from the weir, were tagged in 1960—64. A total of 8,000 smolt were tagged, 1,131 of which were later known to have been recovered in the river or the Baltic sea. The survival of smolts varied between years, 1963 being by far the most favourable, while the cold spring of 1962 gave poor returns. Smolt size was found to influence the recovery rate. The average rate of recovery was 14 %, but in larger smolts of the 1963 class it was 25—40 %. In the figures all the recoveries are presented, even those which made shortly after tagging.

Early movements of post-smolts

In the first three months (May—July), the post-smolts spread slowly along the coast of Skåne, and a few returned to the river (Fig. 1). Some crossed the open sea — one was found in the Gulf of Riga. During the next three months, this tendency became more pronounced. Not only the eastern but also the southern coast of Skåne was followed. Some trout pursued their westward penetration to the Belt area around the Danish islands. A more extended movement started to the northeast, with finds as far away as the Gulf of Finland and north of Åland. Some trout returned to the river in the autumn, having reached a size of 25—45 cm (average 38 cm), most of them probably for spawning and for overwintering. Since the trout were still partly below the minimum size for legal fishing, it is hard to determine the proportions of the different categories.

First winter

During the winter the Verke trout began to be vulnerable to commercial fisheries. From scale readings on tagged and untagged trout the total length, at the end of the first season's growth, was found to be 40 and 41 cm respectively. From November to January the immature trout were spread over vast areas of the southern Baltic. Many were caught around the northern tips of

the islands of Öland and Gotland. From February to April, the tendency for northeastern dispersal was even more pronounced. There were 9 finds in the region from the Gulf of Finland to the Gulf of Riga and 17 trout were taken around Gotland, most of them on the eastern side (Fig. 2). Trout fishing on the margin of the coastal ice was reported from Gotland. Verke trout were, however, at the same time also found some distance west of the home river and even on the Swedish west coast. These trout had followed the north-running sea current through the Öresund strait.

Second summer

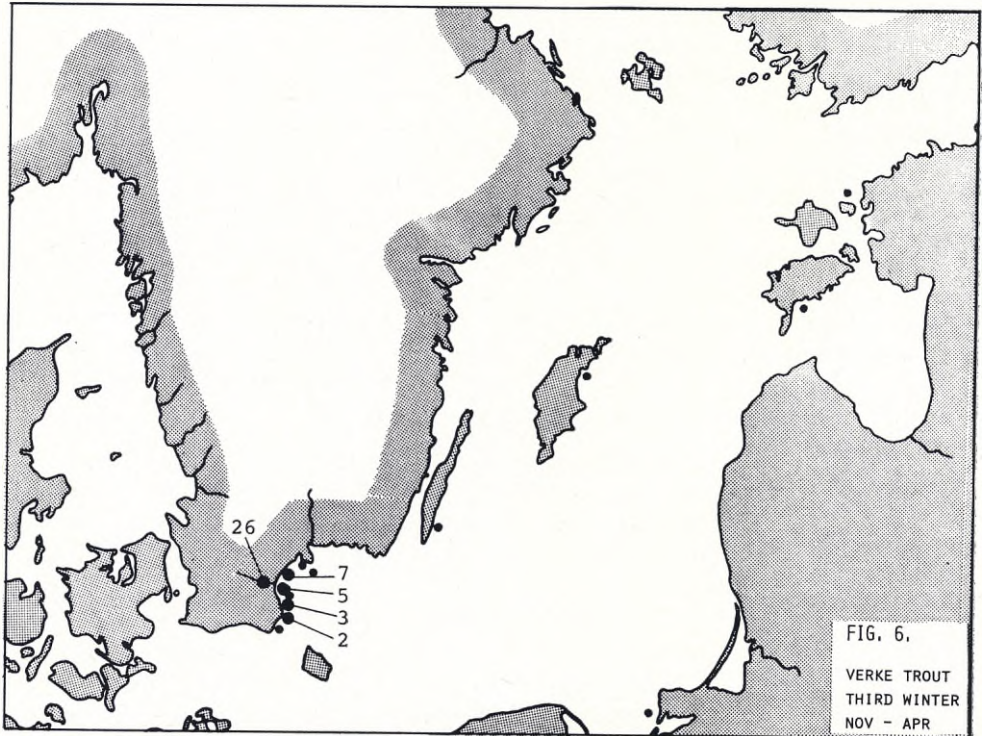
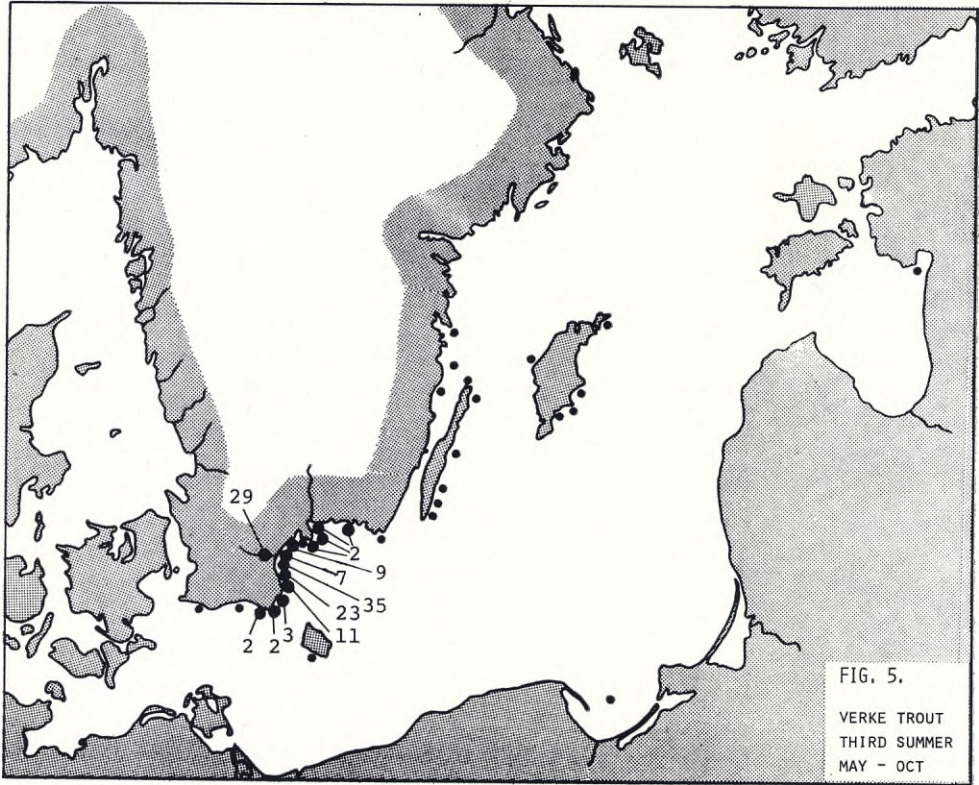
In the spring months seven trout were caught in the Gulf of Riga region, probably having arrived there during the winter. There were few records from Öland and Gotland, or from the Danish islands (Fig. 3). In late summer and early autumn a new burst of trout was reported from Öland and Gotland, and some stray specimens were reported from the Bothnian Sea. All of the Verke trout were by now fully vulnerable to fisheries. The bulk of the smolt-class returned in the autumn for spawning in the Verke River, having reached a size of about 50—55 cm. The still immature trout were, at the end of the second growth season, about 60 cm in length.

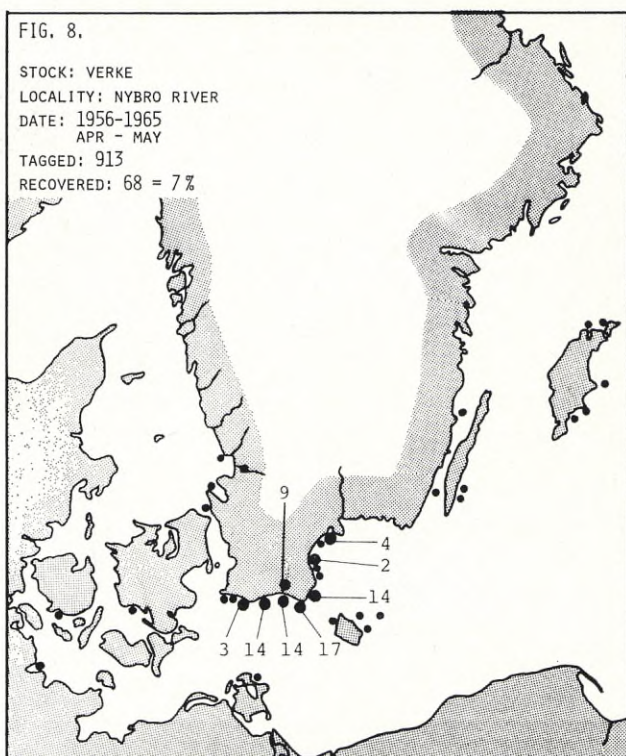
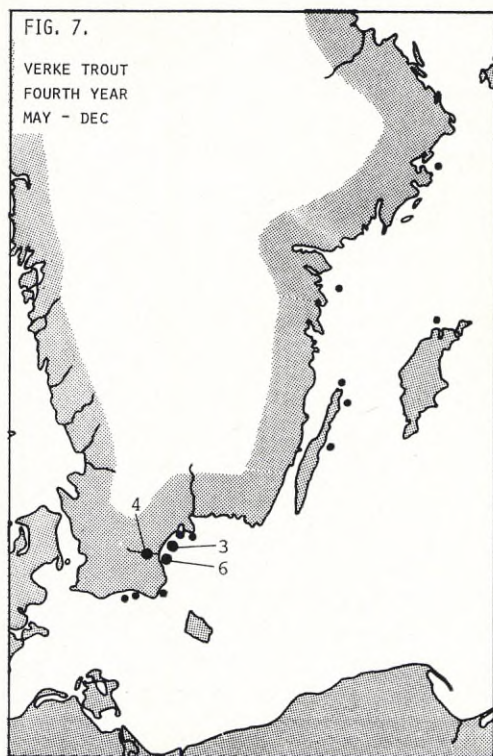
Second winter

Quite a few finds were again reported from northern Öland and eastern Gotland, and some finds were made on the eastern side of the Baltic from the Gulf of Finland down to the Polish coast (Fig. 4). Compared to the very few records from the Danish islands there is clear evidence for the predominantly northeastern distribution of Verke trout.

Third summer

Not a single trout was reported west of Falsterbo (the southwestern point of Skåne), but 14 recoveries were made around Öland and Gotland (Fig. 5). In the autumn the last trout belonging to the smolt-class matured and returned, having reached a size of 65—70 cm. When growth had terminated (calculated from older fish), the total





length was 70–75 cm, and tagged fish were some 3 cm shorter on average than non-tagged fish belonging to the same smolt-class.

Third winter

Most of the trout had returned to Skåne. Not a single find was reported from the west, but five trout were reported from the east (three had crossed the open Baltic) (Fig. 6).

Fourth year in the sea

Most trout were now on their second or third feeding tour in the sea. No finds were reported from the west and six finds were made in the northeast, confirming the conclusions already formulated. No trout had crossed the Baltic to its eastern coast, suggesting that older trout make shorter trips (Fig. 7).

Nybro stream

Nybro is a small stream, emptying on the south coast of Skåne, some 5 km east of the town of

Ystad. It previously had a native trout population, which was wiped out by heavy eutrophication and pollution. A local group of devoted anglers rehabilitated the stream, after cleaning-up operations had made the water quality tolerable for trout. Verke river fry were used and a reproducing population was established in the late 1950's (EHNBOOM 1966).

A total of 913 natural smolts were tagged during 1956–65, and of these, 68 recoveries were reported (7%). Fig. 8 shows that four trout had moved north (with the current) through the Öresund strait, one of which was a straggler running up the Lagan river. Three others were caught in the Danish Belt area, while four finds near Öland and five around Gotland suggest that the north-eastern migratory tendency of the Verke river trout was retained even in the new environment. It should be noted that the recovery rate is only half of that usually obtained for Verke trout tagged in their normal environment. This may suggest increased mortality and/or some confusion

in homing. The Lagan straggler has no single counterpart among the 1,100 recoveries of Verke trout tagged in their home stream.

Hatchery smolts of the Verke stock

Råneå

In May 1969 about 1,200 Verke trout were released outside the mouth of the Råne river, almost at the top of the Bothnian Bay. Later some 14 % of the fish were reported (Fig. 9). The main result of this experiment is the pronounced tenacity shown by the trout in remaining close to the point of release (140 of the 167 recoveries). Seven fish ascended the Råne river and 22 ascended the adjacent, and much bigger, Lule river. The tenacity of these trout as well as the number of non-homing stragglers stands out in contrast to the behaviour of Verke trout in their normal surroundings.

Lule river

660 Verke trout were released on May 19 and June 25, 1964. Like the Råne fish they were raised at the Boden hatchery, near the point of release. Again, their extreme tenacity stands out as the main result of the experiment: 170 trout were recaptured in the Lule river or in the area close to its mouth. A few trout moved short distances along the coast (Fig. 10). Atlantic salmon smolts, annually released in the Lule river, regularly move south to the southern part of the Baltic Sea. The Verke trout, known for their long-distance movements in the southern Baltic, thus here behave in a manner which is strikingly different from that of Atlantic salmon.

Skellefte river

Two experiments, from May 1964 and May 1967, are summarized on the map. A total of 950 trout were released, 15 % of which were later reported. 28 trout were found in the Skellefte river, and another 65 were recovered just south of the river mouth (Fig. 11). There was some dispersal along the coast, mostly to the south, but also to the Finnish coast. On the whole the migratory activity was fairly low. These fish were raised at Kvistforsen hatchery, situated on the river.

Ångermanälven river

A batch of 1,000 smolts was released on May 12, 1964. Later, 308 trout (31 %) were reported, 104 of them in the river, to which many had homed. Dispersal along the coast was obvious, all the way from the Ume river in the north to the Dalälven river in the south. Straggling fish ran the Lule river (one specimen) and the Indal river (one specimen). Two specimens crossed the sea, presumably along the narrow Kvarken route (between the Bothnian Sea and Bothnian Bay). One single trout was reported north of Åland (Fig. 12). These trout were raised at the Forsmo hatchery, situated on the river.

Dalälven river

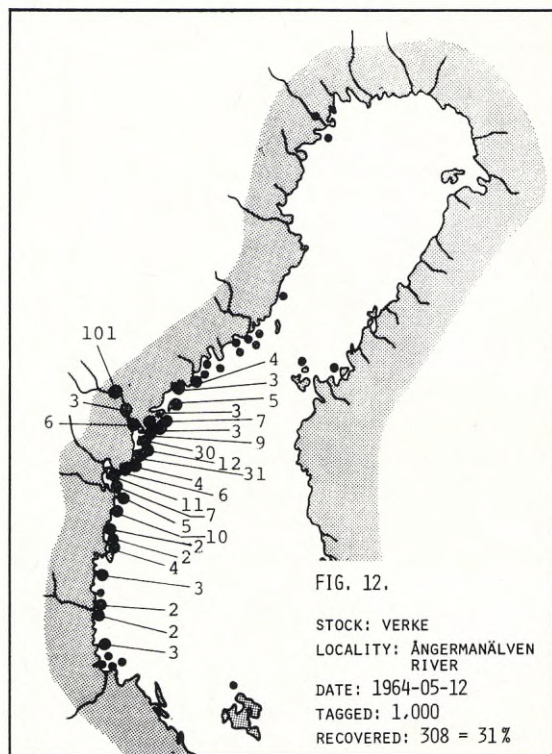
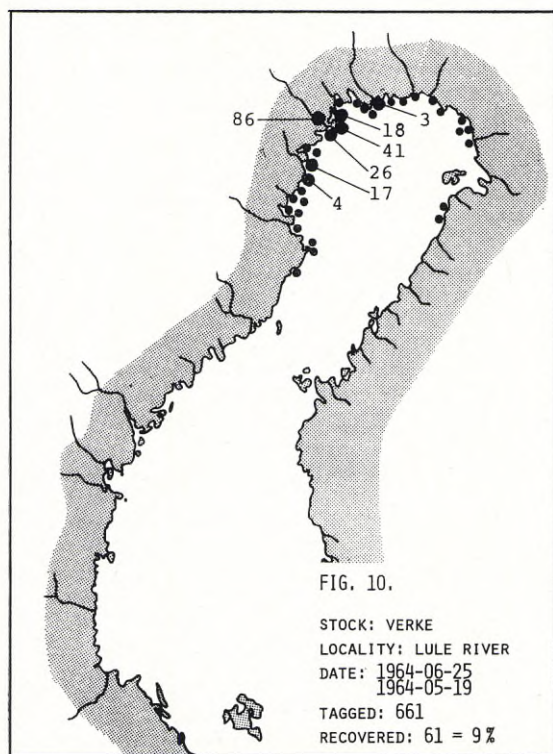
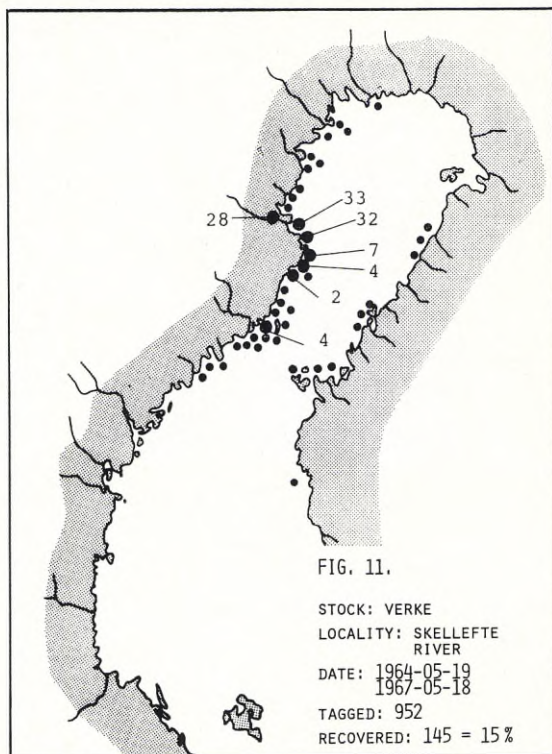
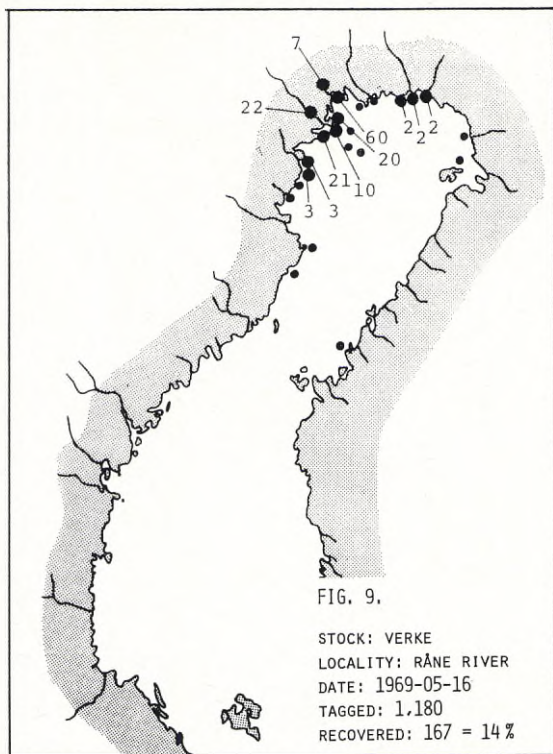
Two stocks of Verke trout were raised at the Älvkarleby hatchery and released as two-year olds in early July 1965 (unfortunately too late in the season). One was the resident stock, which normally lives above the impassable waterfalls, the other the ordinary sea-running stock.

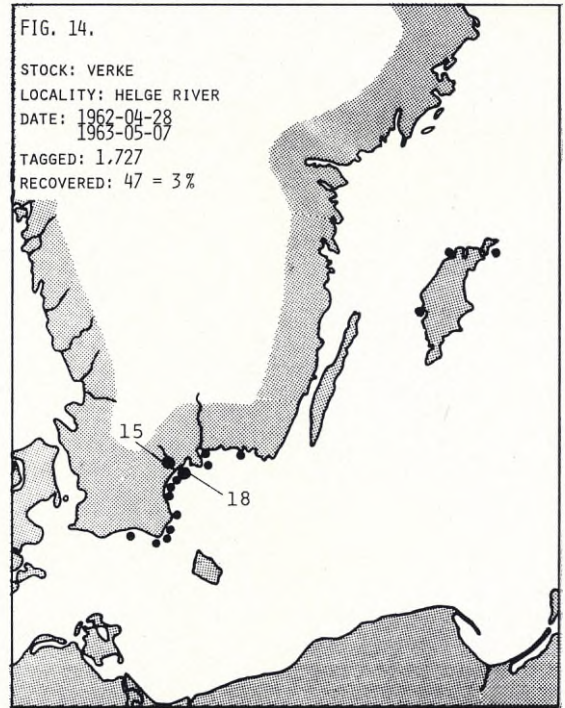
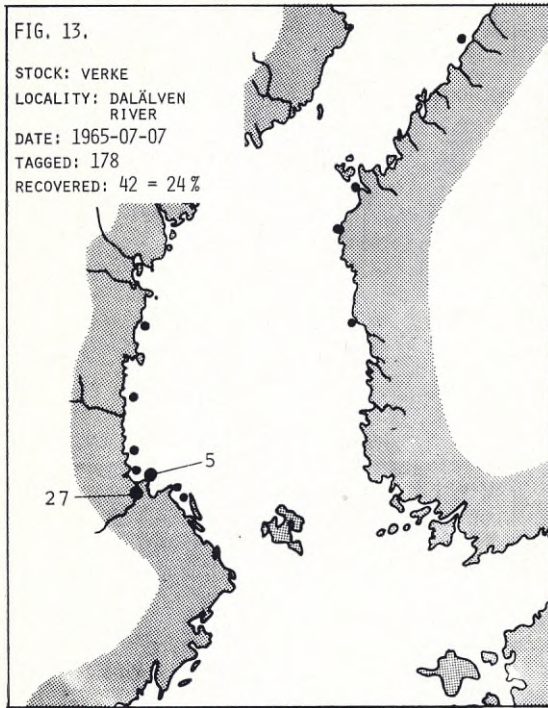
185 tagged resident trout produced 46 recoveries, or 25 %. 42 were found in the river, three were found in the estuary and one single trout was caught at the town of Vasa, Finland. Out of the 42 trout reported from the river seven had probably, to judge from their size when caught, spent some time in the estuary or the sea.

178 tagged migratory trout produced 42 recoveries, or 24 %. 27 were caught in the river, and about half of them had spent some time in the estuary or the sea, to judge from their size. Five trout were caught in the estuary. Two were reported on the coast just south of the river mouth, and four others were reported some distance northwards along the coast. The last four had crossed the sea in a northeasterly direction and were reported from Finland (Fig. 13). Although the material is small, it suggests that the two stocks had different migratory behaviour when both were released in a river much larger than their native Verke.

Helge river

Two batches of Verke smolts, 1,700 in all, were released in the mouth of this Skåne river in April 1962 and early May 1963. They had been raised





at the Älvkarleby hatchery. Recoveries were few, only 47 trout or 3 % were reported. 15 were caught in the river and a further 18 were caught close to the river mouth. There was some slight dispersal along the coast and there were three long-distance movements to Gotland (Fig. 14).

Verke river

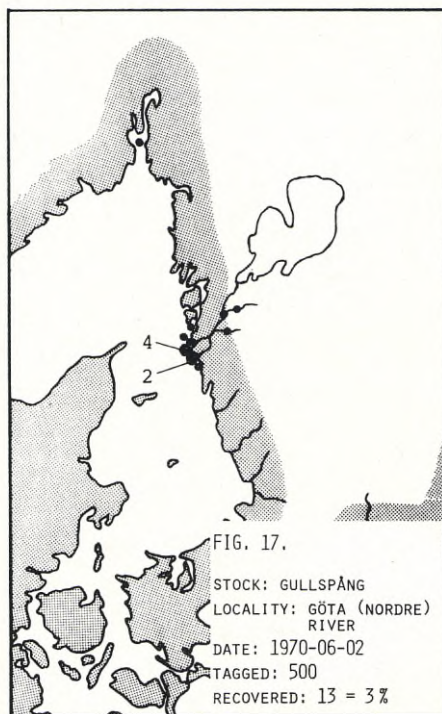
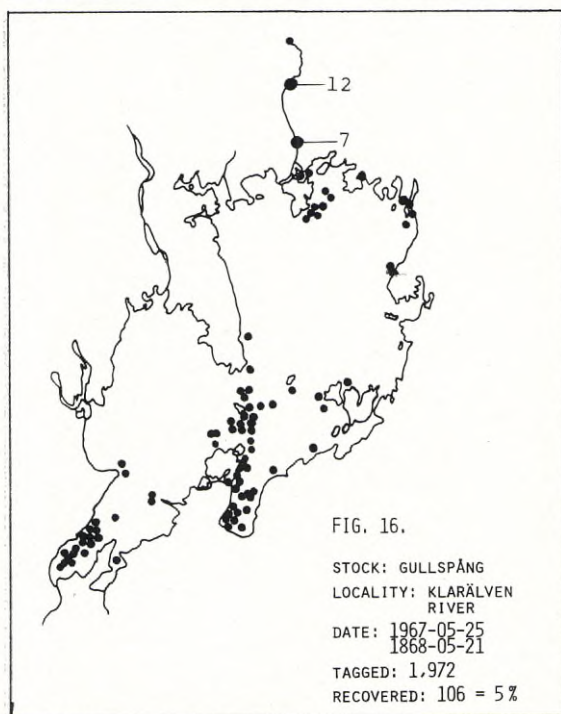
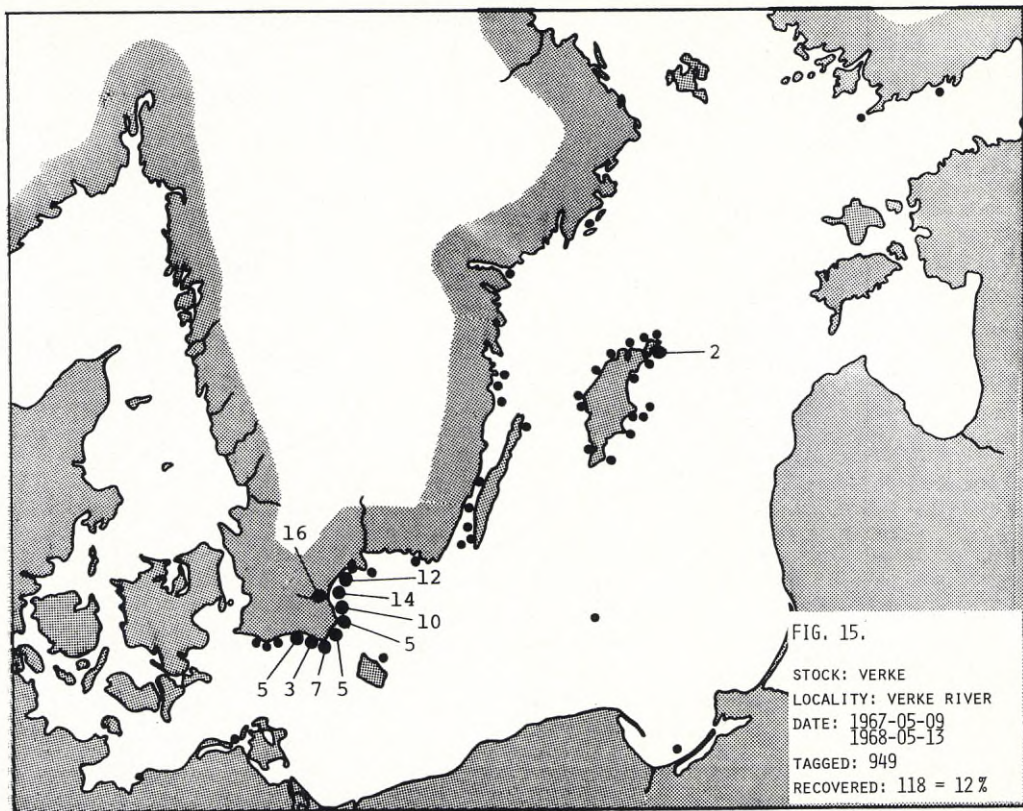
In early May 1967, and again in 1968, batches of Verke trout smolts (migratory stock) were released in the mouth of their home stream, after having been raised at the Älvkarleby hatchery, 700 km away. The recovery rate, 12 %, was slightly less than that for natural smolts (14 %). However, the distribution of the trout was normal for the stock (Fig. 15). The general predominantly northeastern tendency is clear, with 17 trout found around Gotland, two in the Gulf of Finland, 11 more along the Swedish east coast (from Öland and northwards), while not a single trout was reported west of Falsterbo.

Summarizing the evidence obtained by these experiments it can be stated that Verke river migratory trout behave as if they have an inborn

tendency to move NE. This tendency can be blocked by coasting behaviour, which results in a dispersal mainly determined by the local topography. This coasting behaviour might in turn be almost reduced to site tenacity if the trout are transplanted to the northernmost part of the Baltic Sea (the Bothnian Bay), where the water is very brackish (2—3 promille) and the temperature is low, even in summer.

The Gullspång trout

There are several trout stocks in Lake Vänern, spawning in the tributaries and feeding on smelt and cisco in the lake. Originally, large-sized trout also spawned in the mighty outlet, the Göta river just upstream of the waterfalls near the town of Trollhättan (LLOYD 1854), but this stock was probably wiped out by the damming of the lake. Another stock of large trout, which ran the Gullspång river (RUNNSTRÖM 1940), was almost exterminated by hydroelectric damming. However, due to the energetic work done by ROS (1966) it may now be possible to save this stock. As part of the restoration project, the Gullspång



trout has been propagated in various hatcheries, and it was released in northern lakes and along the Baltic coast in order to test its presumed inherent excellent growth capacities and to enlarge the supply of eggs. It was found to be one of the five best trout stock producers by LARSSON et al. (1979).

Lake Vänern

For various reasons hatchery smolts have so far not been released in the native Gullspång river. In the years 1967—68, a total of 1,972 Gullspång trout smolts were, however, released in the lower part of the Klarälven river, at the northern end of the lake. They were raised at the Brattfors hatchery. The number of recoveries was low, only 106, or 5 %. The finds were dispersed throughout the huge lake, with a concentration of finds in two southerly bays (WICKSTRÖM 1974) where food was probably most abundant (Fig. 16). The general impression of the dispersal might also be interpreted as a downstream movement, caused by the known current pattern in the lake. One trout was found in the outlet, suggesting that some trout might have drifted out of the lake, though no tagged trout were reported from the lower Göta river or the west coast. However, this result prompted the next experiment.

Göta river (Nordre river)

500 tagged Gullspång trout, from Brattfors, were released in June 1970. Later, 13 trout, or 3 % were reported as caught, all but one found locally in the river or the estuary (Fig. 17). The exception was a trout caught in the Oslo fjord, Norway. This trout had obviously drifted with the strong 'Baltic current' which runs north along the Swedish west coast. The tagging of native west coast trout has shown northward drifting (BERNTSSON and JOHANSSON 1977), and the same result was observed when one-year-old rainbow trout were released (GÖNCZI 1965). West coast trout and rainbow trout were in fact found all along the Norwegian south and west coast as far north as the town of Bergen.

The low recapture rate for Gullspång trout suggests poor survival in the saline seawater on the west coast, which is not surprising for a freshwater stock. It may also explain why no Gull-

spång trout from Lake Vänern were reported from the west coast, though some may have drifted down the Göta river.

Dalälven river

The Älvkarleby hatchery was involved in the operations to save the Gullspång trout and produce eggs. Fin-cut and/or tagged smolts were released in the river, and eggs were secured when the trout homed back to the hatchery after their feeding movements in the sea. Over the years (1965, 1970, 1971) totally 1,700 smolts were tagged and 190 (11 %) were later caught on the coast, in the sea or in the trap at the Älvkarleby hatchery (Fig. 18).

The dispersal of the Gullspång trout in the Baltic was extensive. They spread north along the Bothnian coast (one straggler ran the Indal river), traversed the Bothnian Bay to the Finnish coast, and drifted south and were caught, pelagically, by the commercial salmon fishermen operating in the open Baltic Sea. Others were found along the coast of Skåne, off the Danish island of Bornholm and off the Polish and Lithuanian coasts. It should be observed that no single trout was reported from the Gulf of Finland or the Gulf of Riga, areas in which so many Verke trout were caught. The main direction of dispersal of the Gullspång trout is therefore 1) along the coast, and 2) to the southern pelagic areas of the Baltic.

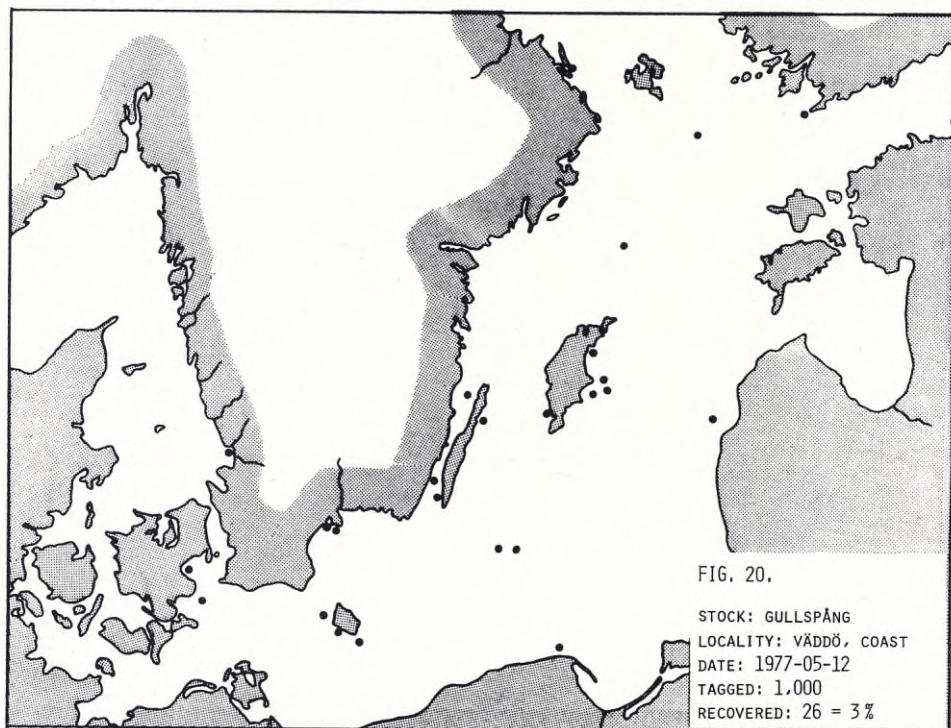
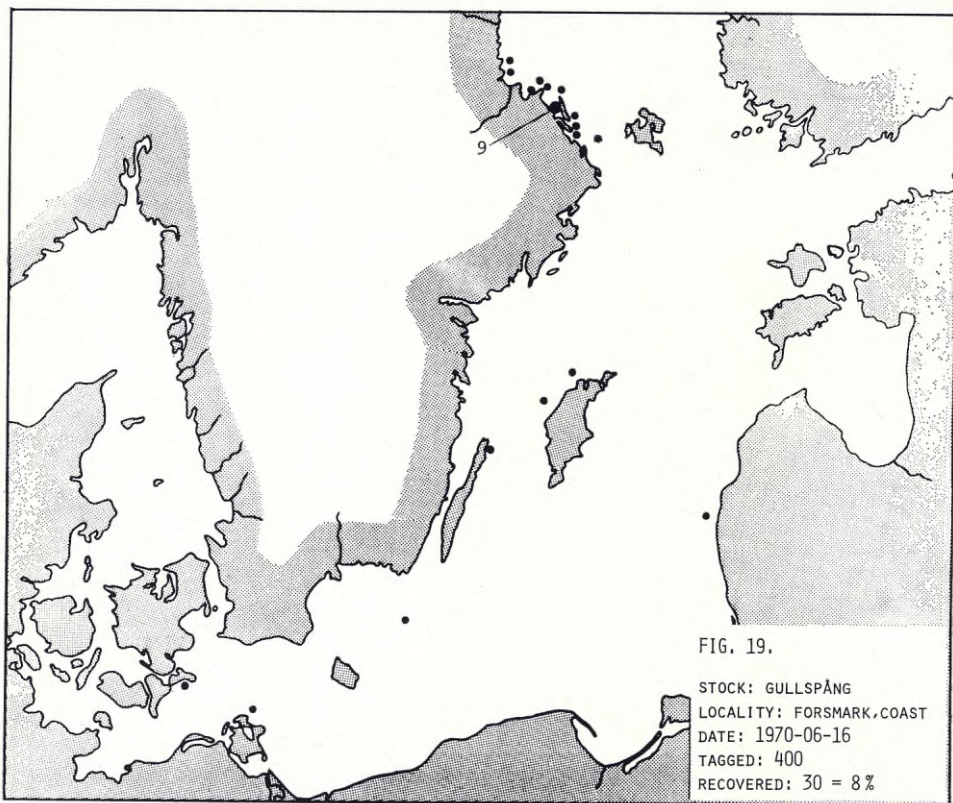
Isle of Vädö, Uppland coast

Two batches of trout were released along the coast, presumably without olfactory contact with river waters. 400 were released at Forsmark, northwest of the isle of Vädö, in June 1970, and 1,000 smolts were released on the eastern side of Vädö (Bylehamn) in May 1977. Recoveries were 30 trout (8 %) and 26 trout (3 %) respectively. The Forsmark fish were to some extent caught in the vicinity of Vädö, while the Bylehamn fish dispersed more thoroughly. Gullspång trout from these experiments (Figs. 19 and 20) turned up in the salmon fishery catches and again demonstrated the pelagical roaming behaviour of this particular stock. Again, the Gulfs of Finland and Riga were without finds, with the exception of one Bylehamn trout, caught at Tvärminne, Finland, in November 1981, after five growth sea-

FIG. 18.

STOCK: GULLSPÅNG
LOCALITY: DALÄLVEN
RIVER
DATE: 1965-1971
MAY - JUN
TAGGED: 1,693
RECOVERED: 190 = 11%





sons. It was a male fish, 73 cm long and weighing 7.8 kg, no doubt searching for a spawning ground.

Bråviken

The Motala river empties into the innermost part of Bråviken bay, but a number of trout experiments have been performed in the outer part of Bråviken bay, where a ferry enables release of the fish in mid-water. One Gullspång trout experiment is summarized in Fig. 21 (there are several confirmatory experiments). In this case 500 trout were released in May 1973, and 129 were later reported (26 %). Apart from 49 recovered in Bråviken bay, most of them homing (as large fish) to the point of release, the others were mostly scattered to the south and, again, many were taken by commercial fishermen in the open sea. Five were reported as being found in the 'southern Baltic' by Danish salmon fishermen.

Tyrislöt, St. Anna

A small batch of 200 trout was released in the archipelago of St. Anna, at Tyrislöt, in early May 1975. The recovery rate was 29 %. Apart from the local finds, six were caught off the small isle of Gotska Sandön in the central Baltic, and others were found by salmon fishermen in the sea mainly south of Gotland. Others appeared along the coast of Skåne, off the island of Bornholm and along the Polish coast (Fig. 22).

Helge river

500 tagged Gullspång smolts started their free life on May 21, 1971 in the lowest part of the Helge river, Skåne. Only 14 (3 %) were later reported, suggesting again a lower rate of survival in a more saline environment. The pattern of dispersal seems to be of the usual type (Fig. 23).

Lule river

This was the only experiment to be performed with Gullspång trout in the northern part of the Baltic. The Lule experiment, started in June 1970, comprised 500 tagged smolts, of which 68, or 14 % were recaptured. They had been raised at the Boden hatchery. Like the Verke trout, transplanted to this cold environment, the Gullspång trout also reacted by showing a similar tenacity

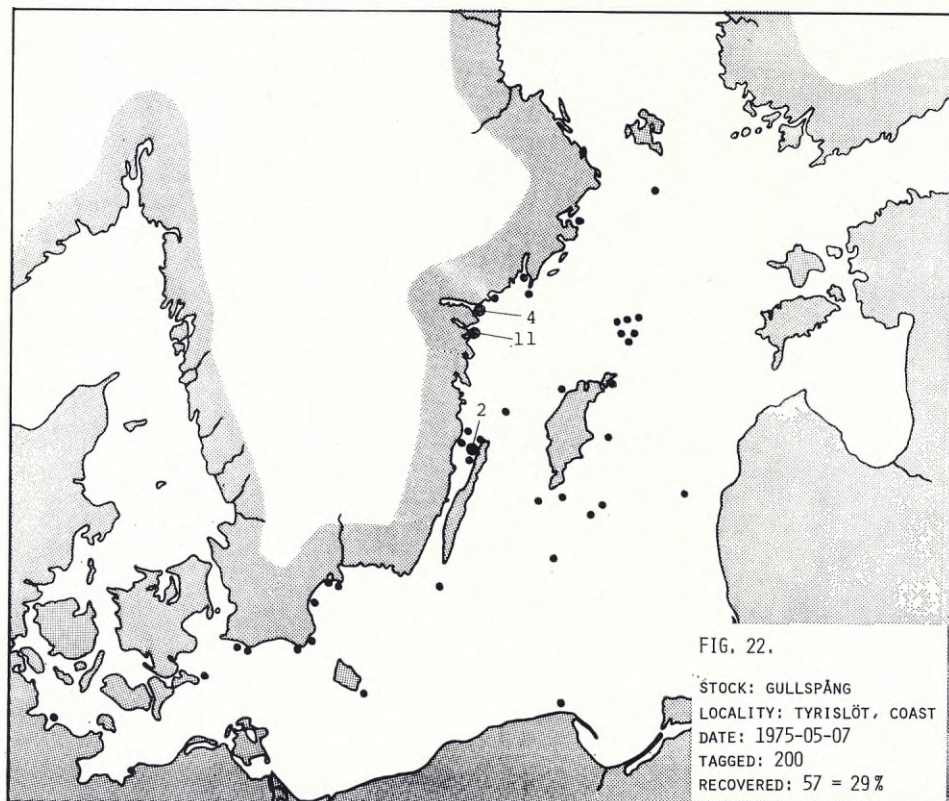
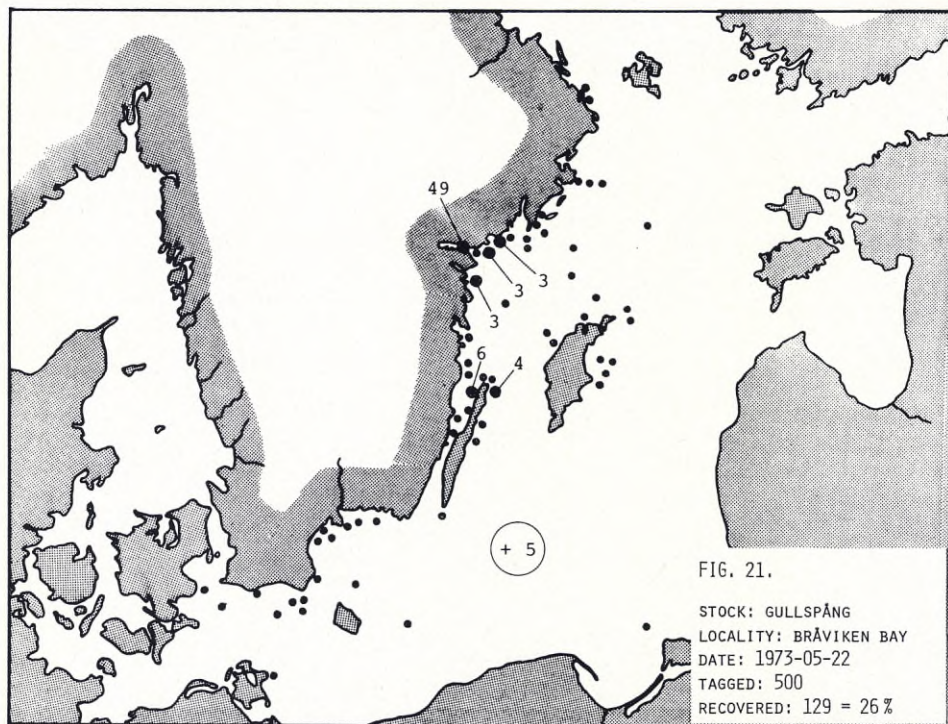
to the coast and the point of release (Fig. 24). 25 trout were reported from the Lule river, and most of the others were found in the vicinity of the river mouth. Two can be said to have dispersed along the coast to the south and 6 dispersed to the north (or traversed the Bothnian Bay). Since there are coastal currents taking the salmon smolts far southwards, it is striking that the otherwise pelagic Gullspång trout did not turn up far to the south, like salmon from the Lule river.

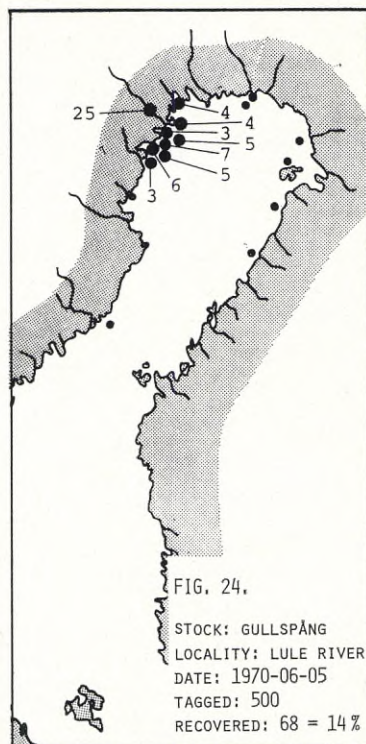
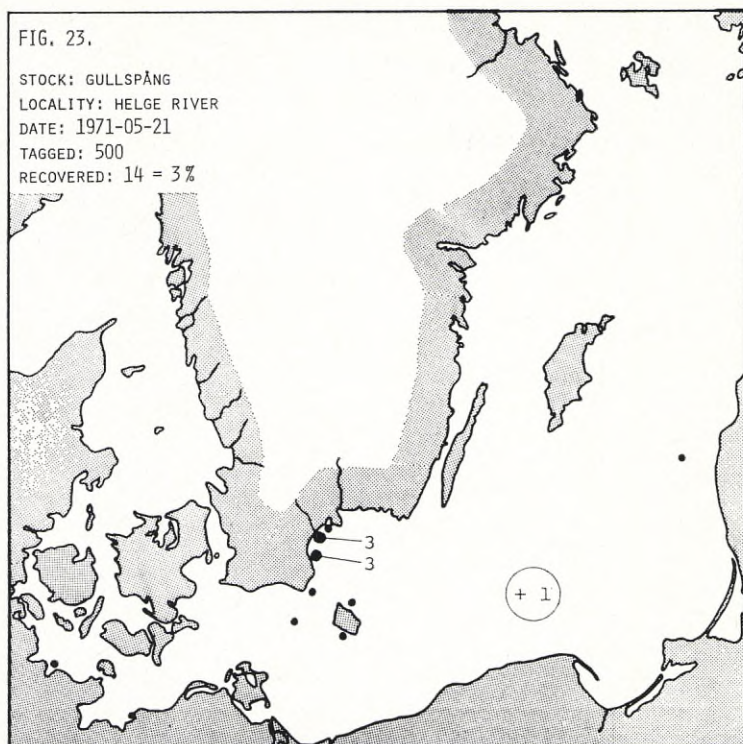
The Dalälven trout

LARSSON et al. (1979) found the Dalälven trout to be one of the five best producers. It has been widely used. Its growth is good, if not as excellent as that of the Gullspång and Wisła river (Polish) stocks. The average recovery rate is consistently high, which is probably correlated to its coastal habits (*vide infra*).

Dalälven river

Many tagging experiments have been performed in the home stream of the stock. On May 18, 1960 two batches, each consisting of 500 smolts, were released. One was released near the village of Älvkarleby, some ten km up the river, and the other near Skutskär, situated on the eastern shore of estuary area. May 18th was the last day of a period of anticyclonic weather with light winds. On May 19—21, a northerly wind was blowing. This wind may have exaggerated the migrational differences between the batches. The Älvkarleby fish were found along the coast, mainly to the north (one fish off Gotland) (Fig. 25). The Skutskär fish were more widely spread: again, most fish moved north along the coast, but two crossed the Bothnian Bay to Finland, four trout appeared far south off northern Öland and another group of four were caught in eastern Skåne. One trout crossed the Baltic Sea to the SE (Fig. 26). The Skutskär fish were obviously more influenced by a south-running coastal current, known to occur along the Swedish coast. Homing was more pronounced in the Älvkarleby fish (90 specimens) than in the Skutskär fish (59 specimens). Of the Älvkarleby trout, two stragglers appeared in the Ljusnan and Ljungan rivers to the north, and of





the Skutskär trout, stragglers were found in the Ångermanälven river (two fish), and in the Emån and Mörrum rivers to the south.

The experiment was repeated in 1966. On May 23, two batches of 500 trout each were released in Älvkarleby and Skutskär. The number of recoveries was the highest on record, suggesting that climatic factors were involved, since exceptionally rich year-classes of other freshwater fish appeared the same spring (SVÄRDSON and MOLIN 1981). There was no northerly wind just following the smolt release and no difference in dispersal appeared between the two batches. Both displayed a coastal spread to the north (Figs. 27 and 28). There was one Älvkarleby straggler compared with five for the Skutskär trout. The recovery rates were 42 % and 52 % respectively. The number of homing fish (*i.e.* caught in Älvkarleby) was 129 and 148 respectively.

Later taggings of the Dalälven stock have produced about 1,000 more recoveries, which confirm the pattern already presented by PUKE and STEFFNER (1964). The main dispersal is along the coast,

to the north. Occasionally, fish cross the Bothnian Bay or move south, and if they do so, they travel a fairly long distance.

Ljusnan river

Of the 500 trout from the Dalälven stock (raised at the Ljusne hatchery) that were released in May 1974 in the lower part of the Ljusnan river, 20 % were later caught. Dispersal to the north was about three times more frequent than dispersal to the south (Fig. 29). 27 trout were found in the river of release, two stragglers were caught in the Dalälven river, two were caught in the Indal river and five were found in the Ångermanälven river.

Ångermanälven river

Fig. 30 shows the dispersal of Dalälven trout released in the lower Ångermanälven river, after having been reared at the Forsmo hatchery. There is a pattern of coastal dispersals of about the same distance, northwards as well as to the south,

FIG. 25.

STOCK: DALÄLVEN
LOCALITY: DALÄLVEN
RIVER
DATE: 1960-05-18
TAGGED: 500
RECOVERED: 149 = 30%

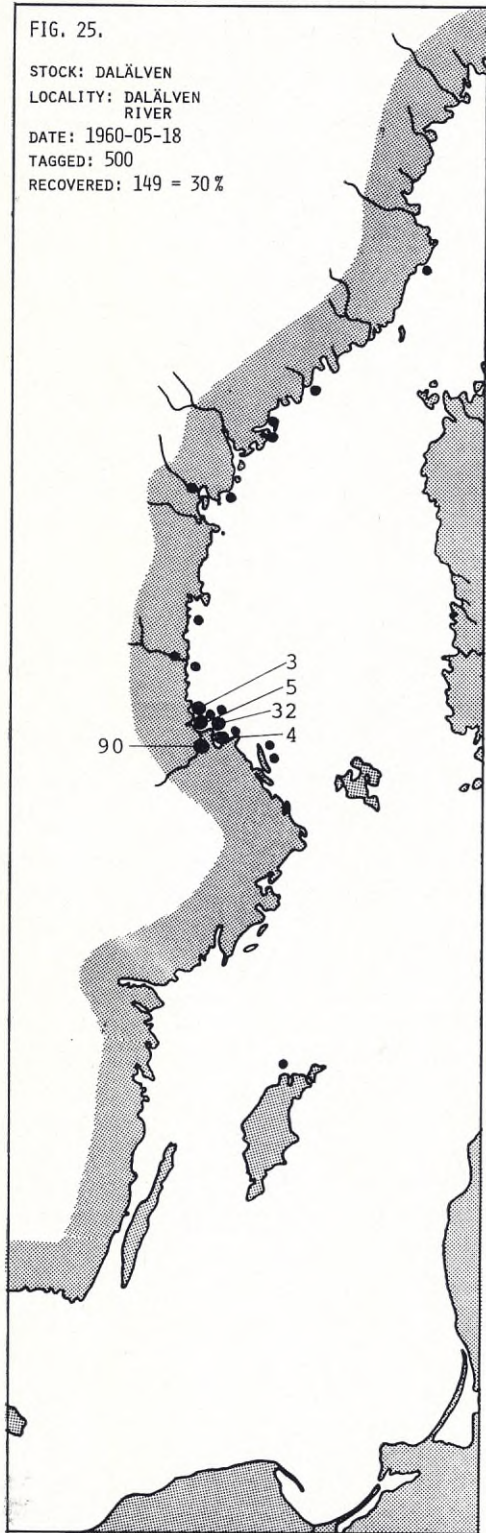
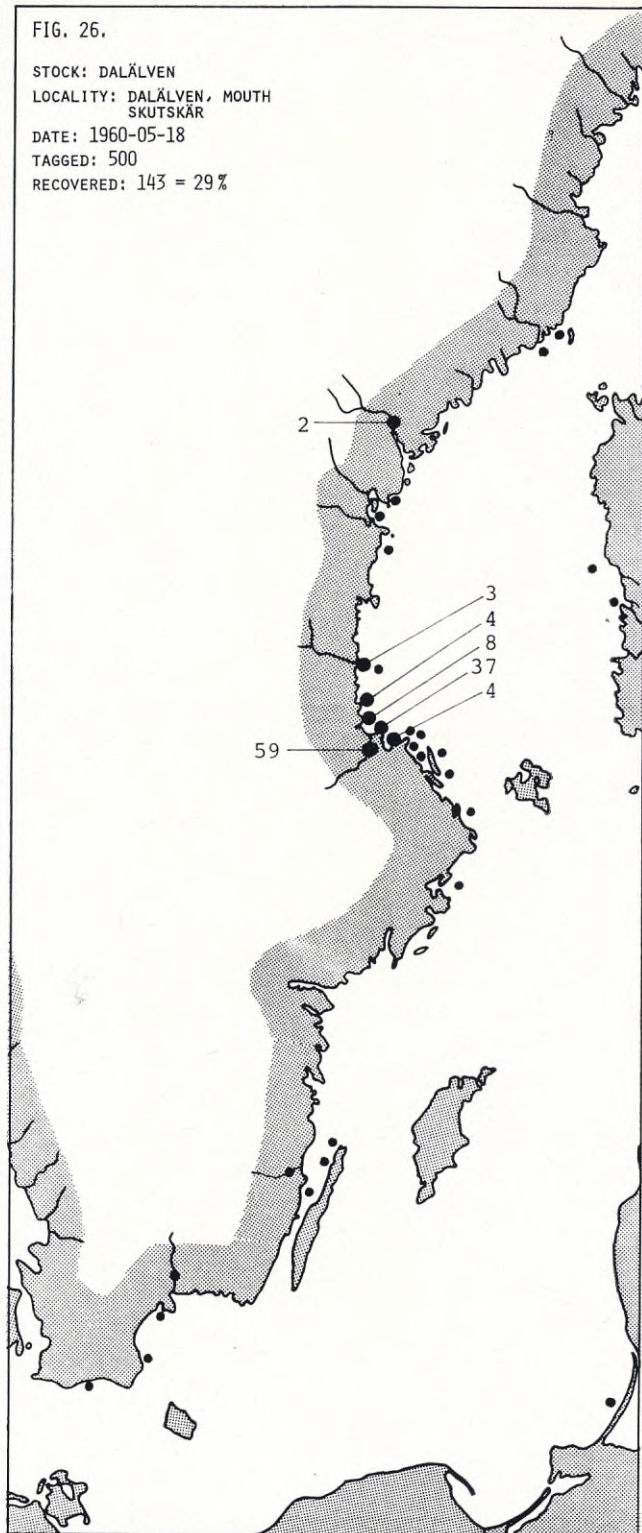
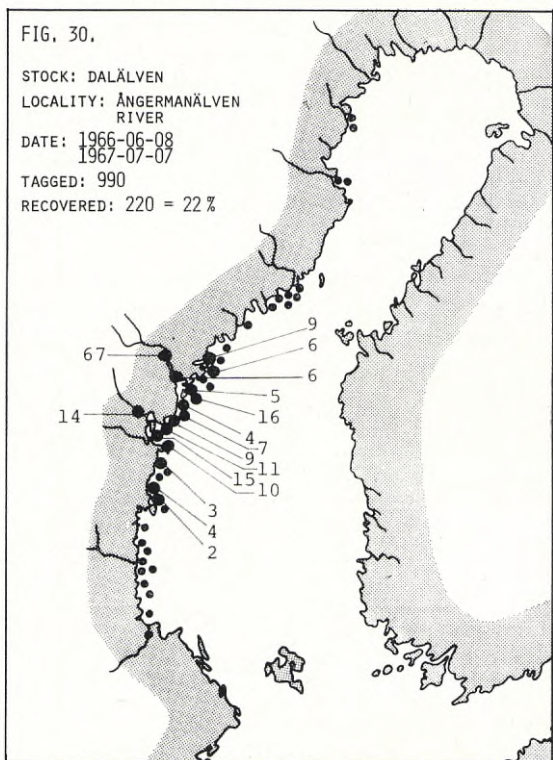
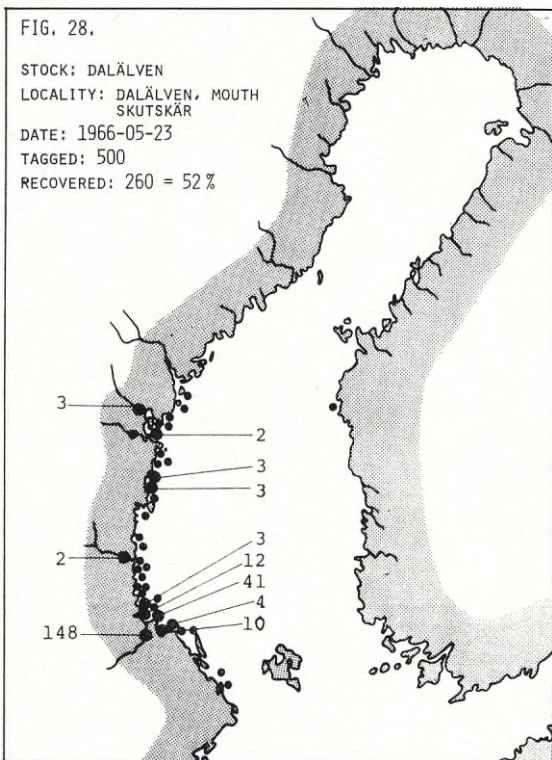
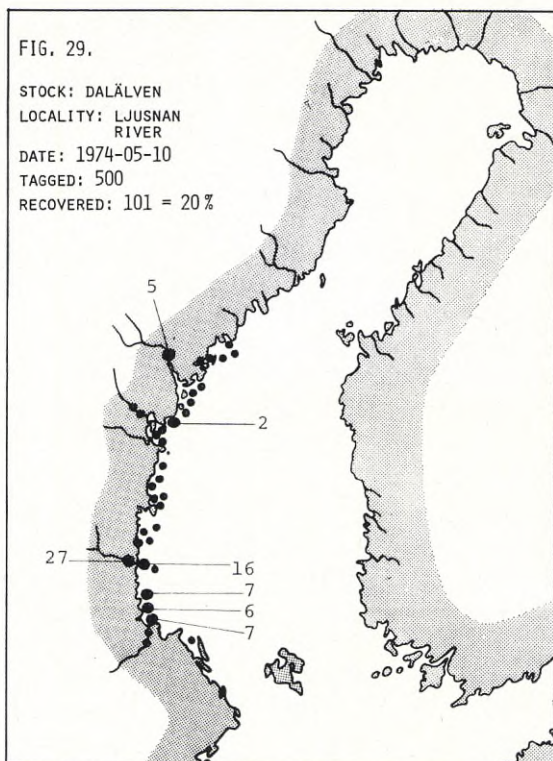
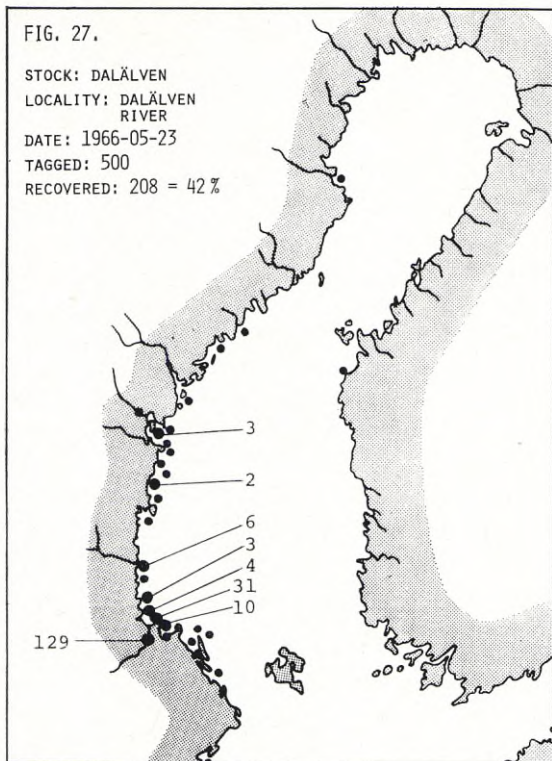


FIG. 26.

STOCK: DALÄLVEN
LOCALITY: DALÄLVEN, MOUTH
SKUTSKÄR
DATE: 1960-05-18
TAGGED: 500
RECOVERED: 143 = 29%





though most recoveries were made in the south. While 67 trout were caught upstream in the Ångermanälven river, another 14 straggled to the Indal river and one ascended the native Dalälven river.

Ume river

For fish released in the Ume river (Fig. 31) there was a fairly even dispersal to both sides of the river mouth. 65 trout were homing (or had never made it to the sea), three entered the Ångermanälven and five the Indal river, while a northern straggler ran the Pite river.

Lule river

A large batch of Dalälven smolts from the Boden hatchery were stocked into the lower Lule river in June 1966. Interestingly, the recovery rate, 30 %, was higher than during the last three experiments, in which it was about 20 %. The year 1966 seems to have generally resulted in excellent survival rates for released salmon and trout smolts, which can be correlated to a late spring with heavy run-off and a hot month of June (SVÄRDSON and MOLIN 1981). The dispersal from the Lule river is mainly to the south due to topographical conditions, and it is slightly larger than that of the Verke and Gullspång trout released in the area. Site tenacity, however, can be said to be predominant. One single straggler ran the Ume river, while 69 were homing and another 63 were caught right in the mouth of the river (Fig. 32).

Summarizing the results of the northern experiments with the Dalälven trout stock, coastal behaviour emerges as dominant. Dispersal to the north is most frequent at first, but this gradually changes to more even dispersal from the point of release. Open sea swimming is obviously very rare. Recovery rates are generally very high and though the trout can be observed to home to any new locality from which they are released there tends to be a significant number of straggling fish, which is also characteristic of the Dalälven stock in its native river.

Bråviken bay

When released from a ferry in the bay of Bråviken, the vast majority of Dalälven trout re-

mained in the area (Fig. 33). Out of 141 recoveries, 127 were made in the bay. The size of the fish suggested good growth in this bay, known for its abundant populations of small-sized herring. Seven fish were found outside the bay where they could have drifted south with the coastal current, as testified by 6 trout found near the Lister peninsula and one found 'on route' in the Kalmarsund strait. The behaviour of the Dalälven trout should be compared to that of the Gullspång trout (Fig. 21) released on the very same day. Both batches were transported to Bråviken from the Älvkarleby hatchery. They display striking evidence of stock traits, the Dalälven trout producing 90 % of the recoveries in Bråviken bay, while 62 % of the recovered Gullspång trout were reported from fisheries outside of Bråviken bay and far away (STEFFNER 1975).

Simpevarp

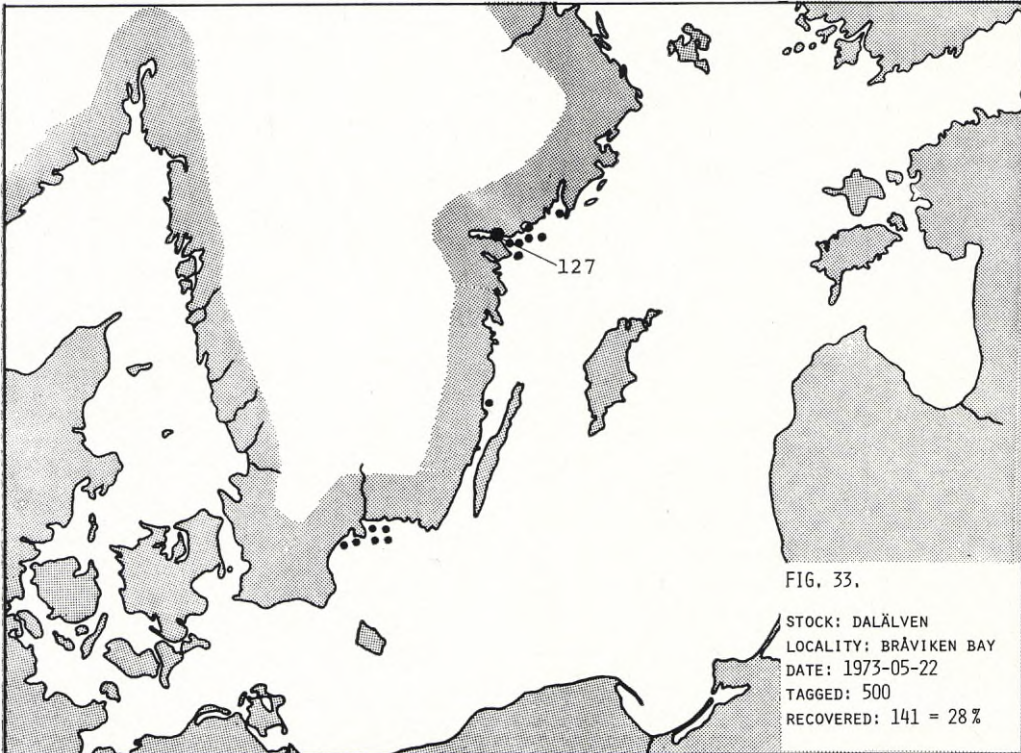
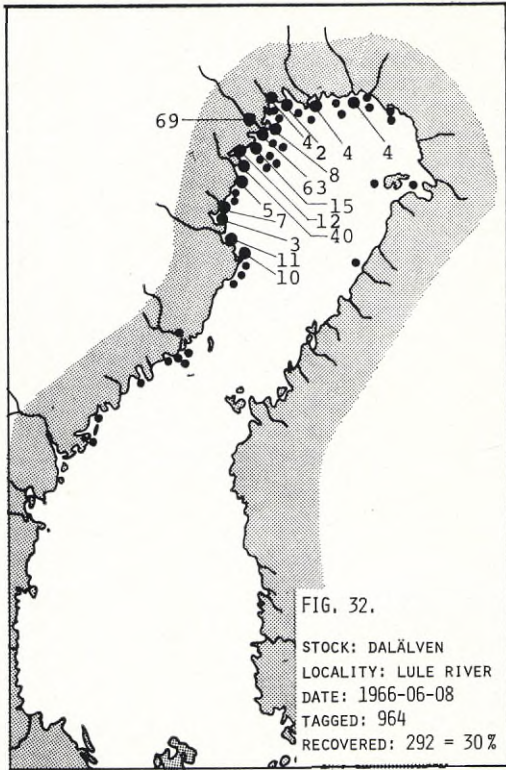
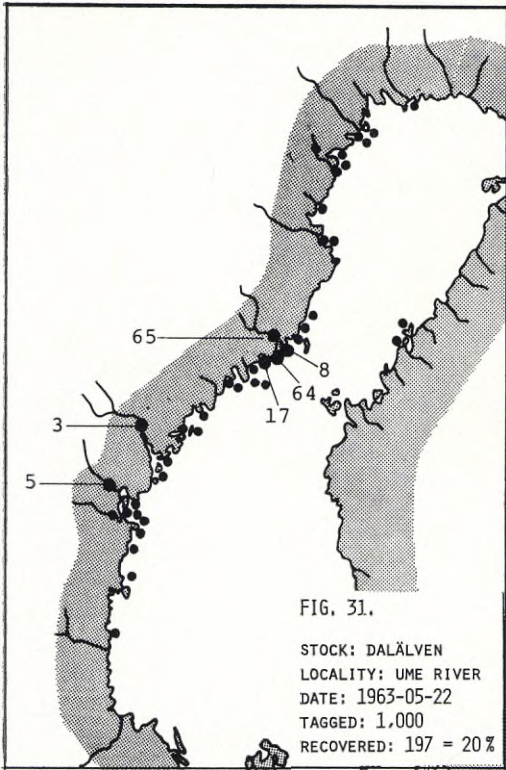
These Dalälven trout were used for experiments on growth performance in heated water from a local nuclear plant. After the termination of the growth experiment some were tagged and released. Fig. 34 shows their coastal behaviour, and in this case their tendency to move north (against the current) becomes evident. Three were found on the coast not far from Stockholm and another four had moved up to the Bothnian Sea, one of them as far as the Ume river area.

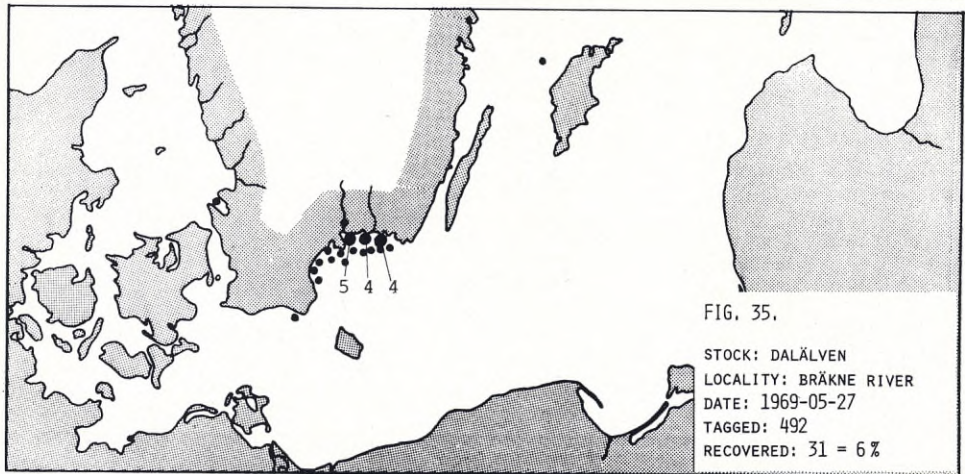
Bräkne river

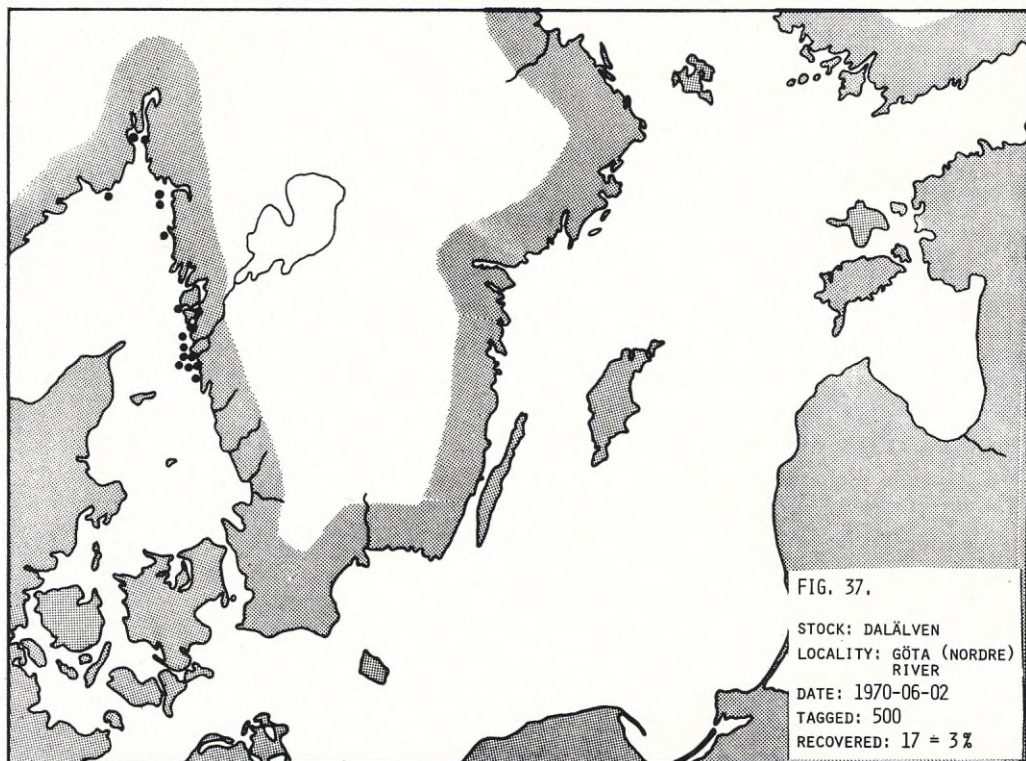
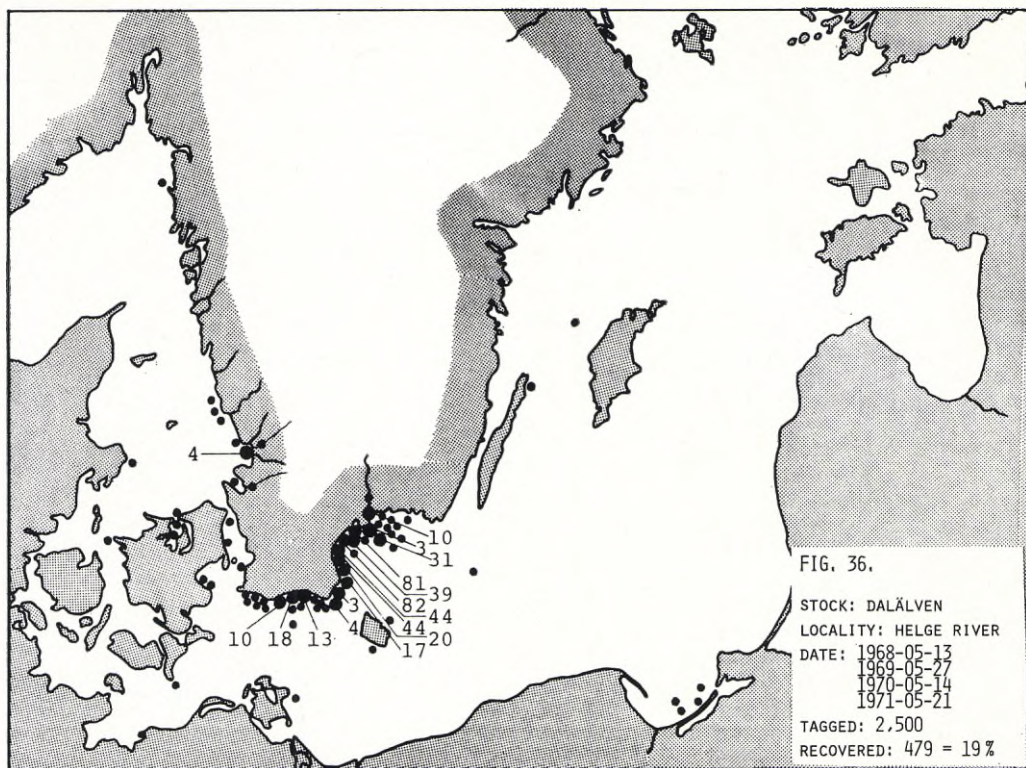
Of some 500 Dalälven trout, raised at Älvkarleby and released in May 1969 at the mouth of the small Bräkne river in the province of Blekinge, only 31, or 6 % were reported. This is a low recovery rate for the stock. Dispersal was very modest, with one straggler found in the Mörrum river. It is tempting to speculate that the shore topography blocked their tendency to move north or drift south (Fig. 35).

Helge river

During the years 1968 to 1971 a total of 2,500 Dalälven smolts were released at this river mouth (Fig. 36). All were raised at the Älvkarleby hatchery. 19 %, or 479 trout were later recovered. Coastal behaviour dominated, and quite a few had drifted north through the Strait of Öresund. One







trout, found close to the Norwegian border, had obviously been transported by the strong west coast current. Stray fish moved to Öland or crossed the Baltic to the Polish coast. Three straggling, non-homing fish were found in other rivers.

Göta (Nordre) river

Like the Gullspång trout (Fig. 17), the Dalälven stock also performed badly when released on the west coast. The recovery rate was only 3 % and the trout drifted to the north with the strong current (Fig. 37). The trout were raised at the Älvkarleby hatchery.

Reliability of the maps

Maps showing recaptured tagged fish are of course dependent on fishing intensity. Some comments on the actual fishing pressure are thus needed.

There are private fishing rights in Swedish fresh waters and along some parts of the Baltic coast, roughly from Gävle down to Karlskrona. The private waters are, however, restricted to a belt of some hundred metres, depending on the depth and the configuration of the shore. Otherwise, fishing along the coast is open to all citizens.

Restrictions in the use of gear are few. Gill-nets are allowed, as are fyke nets, and if a licence is obtained, huge eel traps may be used. Angling is allowed after obtaining personal permission from the land owner, or after purchasing a permit.

On the whole there is intense fishing activity along the entire Swedish coast. River mouths are very heavily fished and salmon and trout stocks are locally overfished by commercial fisheries. The Baltic salmon is mismanaged by fishing far too heavily in the open sea. Therefore trout is caught, not only when moving along the coast, but also by salmon fishermen, on the high seas.

The maps are fully reliable, as far as the general dispersal of trout in Swedish waters is concerned. Along the Finnish and Danish coasts there tend to be similar conditions. In Soviet waters, on the contrary, fishing is more restricted and, above all, the general motivation for, or possibility of sending private reports through the mail is lower. A negative bias is thus suggested for the coasts of USSR, Poland and DDR. The amount of this bias is hard to estimate.

IV. DISCUSSION

There is a contrasting time-scale for the local genetic variation in *Salmo* compared to that of *Salvelinus* and *Coregonus*. Whereas the trout, *Salmo trutta*, has achieved its local diversification post-glacially, the *Coregonus* and *Salvelinus* variation is principally caused by the existence of sibling species, which have introgressed to various degrees in post-glacial times (SVÄRDSON 1979, NYMAN *et al.* 1981).

Sympatric trout stocks with different growth rates and spawning habits are fairly common in larger Scandinavian lakes. Outlet spawners are noted for better growth and larger size, and the divergent behaviour of young fish. The two sympatric trout stocks of Lake Bunnarsjöarna have been made widely known (RYMAN *et al.* 1979). Their genetic difference is calculated to be equivalent to isolation for 125,000 years though they are very similar and show genetic identity at 19 loci (RYMAN and STÅHL 1981).

If the isolation period of 125,000 years is correct, the two stocks should represent two different trout species, since Lake Bunnarsjöarna is not more than 9,000 years old. The calculation is, however, based on the presumed non-selective effect of different LDH-alleles. In fact Lake Bunnarsjöarna is situated in a region of barren lakes and, moreover, char, and not trout, is known to be the species which has spontaneously colonized the uppermost lakes. The fisheries officer of the region, Mr. RICHARD ÖHMAN, does not doubt that the trout were introduced by man, and probably very recently. Different LDH-B-genotypes of *Fundulus heteroclitus* also have been proved to affect the time of hatching as well as swimming endurance (DIMICHELE and POWERS 1982). The Lake Bunnarsjöarna trout thus have little relevance for evolutionary considerations.

In post-glacial times Scandinavia must have been colonized by an anadromous trout, the ecotype from which the other demes have evolved locally. It should be stressed that straggling (non-homing) behaviour was positively selected for during a period in which there were many virgin streams.

CARLIN (1965) summarized the first trout smolt taggings in four rivers of the Bothnian Sea, and



Fig. 38. Surface currents in the Baltic Sea (adapted from Wessel 1971). The salinity is also given, compiled from various sources. The Baltic is brackish and the salinity decreases from 10–15 promille in the southwestern part to 2–4 promille in the northernmost Bothnian Gulf.

found trout to be more coastal and local than salmon, with about 6 % non-homing individuals being caught in foreign rivers.

Three migratory trout stocks, dealt with in this paper, have all been released as smolts in the Bothnian Bay. Their behaviour in this environment has been rather similar. Coastal movements prevail, although the Gullspång trout in other localities tend to drift long distances with sea currents and the Verke trout may also be long distance travellers. The tenacity shown by remaining close to the point of release and the tendency to straggle to nearby rivers suggest a physiological response to the cold water, in which pelagic swimming is a wasteful expenditure of energy.

If this behaviour of the Gullspång and Verke trout is a phenotypic modification due to the environment, the Dalälven trout seems to have adapted itself genetically to its native Bothnian Sea conditions. Compared to the other two stocks, the Dalälven trout tends to stick to its coastal behaviour in all environments tested and, moreover, it displays a consistent trend of having some straggling individuals.

From an evolutionary point of view, the Dalälven stock may be said to be more primitive, more like the presumed early colonizer. Homing can be based on simple olfactory or visual stimuli (cf. BERTMAR 1979).

The more the sea sojourn is extended to increase trout growth and size, the more important becomes the relation of trout to sea currents. Baltic Sea currents are not strong and are mainly caused by the Coriolis' force, combined with the heavy discharge of fresh waters from the many rivers in the north. Winds disturb the pattern and the map by WESSEL (1971), here modified as Fig. 38, is accepted with caution by some specialists (SVANSON, pers. comm.).

However, there seems to be a unanimous opinion that sea currents run north along the Finnish Bothnian coast and south on the Swedish side. TOIVONEN and TUKHUNEN (1975) found that Finnish tagged trout have a northern trend in their dispersal, *i.e.* they move *with* the current, in contrast to salmon, which move *against* it. The Dalälven trout also have a northern dispersal tendency, which, however, runs against the prevailing current (Swedish Bothnian salmon post-smolts

then move with the current!). The behaviour of the Dalälven trout could best be explained by a tendency to slowly disperse against the current when in contact with the shore, but to drift with the current if they loose contact with the shore (cf. the Skutskär result in 1960 Fig. 26).

Fig. 38 shows the mouth of the Dalälven river pointing north, while the provinces of Uppland and Södermanland protrude as a broad eastern promontory into the Baltic. The southern part of this promontory is further split up into a vast archipelago of thousands of islands. Dalälven trout, which drift (as in 1960) south of the promontory, tend to move long distances and might very well have more difficulties in homing than trout which move directly northwards from the river mouth. North-dispersing Dalälven trout also may find several alternative rivers suitable for spawning, while this is not the case for those drifting south. On the whole, the argument for a local natural selection, which determines the contra-current coastal behaviour of Dalälven trout, has some strength.

The Gullspång trout live in the more restricted habitat of Lake Vänern. There are very few rivers offering spawning grounds and, above all, predatory pike abound in the lake. Northern pike (*Esox lucius*) is known to be a formidable predator on *Salmo* and *Salvelinus* all over Scandinavia, and trout live in small Baltic streams only in those areas where pike are rare or non-existent.

The natural selection caused by pike, must have produced the tendency of Gullspång trout smolts to minimize the time spent as parr in the river (cf. RUNNSTRÖM 1940, WICKSTRÖM 1974), and to head out into the huge lake to lead an off-shore pelagic life, where pike are few (although they do exist as large-sized specimens). As a result the Gullspång trout should have evolved a homing capacity, after having spent their growth period in open water with negligible contact with the shore.

The Gullspång trout used in the experiments were extremely pelagic and drifted widely, in all environments except the cold Bothnian Bay. In spite of the long distances covered, the evidence (admittedly indirect) is that homing was good. The prolific egg production at Älvkarleby was based on the fact that large-sized Gullspång trout

Table 1. Total length of recaptured trout of the Verke stock in five experiments. All were released as two-year-old hatchery smolts. Growth is more rapid in the southern Baltic Sea, where trout, released in the Verke river, migrate.

Area/River	cm	Year 1	Year 2		Year 3		Year 4	
		2nd half	1st half	2nd half	1st half	2nd half	1st half	2nd half
Råne 1969	20—29	6	—	—	—	—	—	—
	30—39	32	3	10	1	1	—	—
	40—49	—	1	35	3	3	1	—
	50—59	—	—	2	1	15	—	3
	60—69	—	—	—	—	1	—	11
	average	33.4	37.5	43.3	45.0	53.0	45.0	62.9
Lule 1964	20—29	26	4	1	—	—	—	—
	30—39	26	26	29	4	4	—	—
	40—49	1	3	30	5	5	1	—
	50—59	—	—	4	6	11	1	—
	60—69	—	—	—	—	2	—	—
	average	30.3	34.7	40.1	46.3	50.0	50.0	—
Ängermanälven 1964	20—29	37	6	1	—	—	—	—
	30—39	36	37	14	—	—	—	—
	40—49	2	8	21	8	—	—	—
	50—59	1	—	11	4	12	—	—
	60—69	—	—	—	—	8	3	6
	average	30.7	35.4	43.9	48.3	59.0	65.0	65.0
Dalälven 1965	20—29	4	—	1	—	—	—	—
	30—39	1	1	4	3	1	1	—
	40—49	—	—	5	5	1	2	—
	50—59	—	—	1	—	3	—	—
	60—69	—	—	—	—	—	1	—
	average	27.0	35.0	40.5	41.2	49.0	47.5	—
Verke 1967	20—29	2	—	—	—	—	—	—
	30—39	9	10	1	—	—	—	—
	40—49	4	15	3	—	2	—	—
	50—59	1	5	22	3	3	2	—
	60—69	—	—	11	7	3	—	—
	average	37.5	43.3	56.6	62.0	56.2	55.0	—

(no doubt having spent their growth period in the sea, and presumably far away) did return in great numbers to the trap at the hatchery.

Two different trout stocks inhabit the Verke river. The stock living above the impassable falls has an even sex ratio in all age groups, while the stock living below the falls has a very unbalanced ratio after the females have left the river as two-year-old smolts. Females constitute some 75 % of the smolts and also dominate among the ascending adults (SvÄRDSON and ANHEDEN 1963 b). Since any smolt produced by the upstream stock, will be lost to the population, selection has obviously almost eliminated smolt behaviour.

When released near Älvkarleby in the broad Dalälven river, the upstream stock performed some downstream movement, but differed from the anadromous Verke stock by showing much less coastal or sea dispersal. The behavioural differences thus must have, as supposed, a genetic basis.

The anadromous Verke trout smolts may reach the Gulf of Finland (their ultimate target, as taggings suggest) *with* the sea currents after having reached the Bornholm area, if they move counter-clockwise in the southern Baltic and northwards along the Latvian and Estonian coasts (Fig. 38). However, the recovered trout do not suggest such a route. Instead, the finds indicate a more direct

NE-trend, and recaptured trout around Öland and Gotland abound. Selection as a result of fisheries cannot explain the paucity of open sea finds, as the Gullspång trout recoveries show. Instead, the probable route implies a complicated reaction, with the trout mainly moving against currents on their way to Gotland, and with the currents for the last part of their journey. It seems better to assume another mode of movement, e.g. the trout swimming, during the morning peak of activity, against the rising sun, trying not to be swept too far away from the shore. The well-known 'coasting' of migratory birds, continued as long as the guiding line does not conflict too heavily with their inborn standard direction, comes to mind as a parallel.

There are several facts that could combine to create a natural selection for an inborn NE trend of movement in Verke trout. The coastlines of Skåne and the Danish isles provide a most complicated pattern for the trout moving west (as some do). If the trout passed the point of Falsterbo, they would easily be swept away by the strong surface current of brackish water running north through the Öresund strait. If so, the trout would soon arrive in the much more saline habitat of Kattegatt and Skagerack. Native Swedish west coast trout are notorious for their small size and short periods of growth (LINDQVIST 1958, BERNTSSON and JOHANSSON 1977). A Verke trout, successfully homing from the Swedish west coast would most probably be a considerably smaller fish, with fewer and even smaller eggs. On the contrary, growth in the southern Baltic is rapid (Table 1) and some of the largest sized trouts in Europe (outside fresh waters) are found in this area (NALL 1930, ZARNECKI 1963, SVÄRDSON 1967), notably the Wisła, Em and Mörrum stocks.

The southeastern point of Skåne (Sandhammaren) may, to some extent, be a parallel to the waterfalls of the Verke stream. Trout passing it 'downstream' (*i.a.* westwards) risk a smaller chance of homing and, if they were successful, they would risk being smaller and having fewer eggs, and thus being less fit than trout coming from the Öland-Gotland-Gulf of Finland route. The latter are favoured by dense herring prey populations and iso-osmotic waters, in which they waste no energy on osmotic regulation. If homing is also

facilitated by using this route, selection pressure should be strong.

The general picture emerging from these Baltic Sea trout experiments is that the migratory pattern may be lost (Verke upstream stock), consist of coastal dispersal with some incidence of straggling (Dalälven stock), consist of open water drifting in currents with excellent homing behaviour (Gullspång trout) or, finally, be a long-distance directed movement, irrespective of currents, with some contact with shore (Verke downstream stock). In all cases there is evidence that the behaviour has evolved under natural selection in post-glacial times.

BAMS (1976) proved a genetic influence in the homing of pink salmon (*Oncorhynchus gorbuscha*) by testing the effects of paternal genes in two lots of transplanted fish. HORRALL (1981) recently summarized the literature on homing. If homing and genetic isolation evolve together (LEGGETT 1977) it seems that the cues used for orientation could probably be slightly different in various local stocks, where selection favours one out of several potentially available cues common to all fish.

It is not only in early post-glacial times that straggling, rather than homing, should be selected for, but also when advancing glaciers push trout populations south to streams which provide refuge. The trout, as a species different from the Atlantic salmon, has probably lived through several glacial periods (*cf.* SVÄRDSON 1979). Hence, homing correlated to elaborate feeding migrations, has probably repeatedly been alternatively selected for or against. Consequently, the potential for rapid deme radiation to different environments, or withdrawal to a standard sea-running type of behaviour should ultimately have been selected for and determined the ecological niche of the species.

V. MANAGEMENT ASPECTS

Fisheries managers are generally cautious not to destroy natural stocks by the release of foreign fish. In the management of Swedish Baltic salmon this principle has been strictly adhered to during the postwar period. For trout, however, this practice has been less prohibited. This may be due

to the fact that trout stocks abound, that trout has more often been handled by private owners of fishing rights, or that large amounts of trout fry were already transported and released in the 19th century.

Even so, the large-scale transplantations of trout reported in this paper may horrify some fishery managers, and the risks of contaminating stocks may be judged as being too high for winning some scientific results. It should be stressed again, that the activities were started for practical purposes, and aimed to achieve a higher trout production than natural reproduction could provide.

The results do have some considerations for future management. Local stocks are adapted, and may therefore have the best survival odds and be the most efficient homers. On the other hand, there are more or less fast-growing stocks. The Dalälven stock will produce local recoveries while the Gullspång trout stockings may benefit fisheries far away. The Verke upstream stock has been used in river reservoirs, where other stocks have emigrated downstream and been lost to the local reservoir fishery.

The negative effects of the genetic contamination of stocks should not be too strongly emphasized. Natural selection will restore fitness. The general experience from *Coregonus* and *Salvelinus* sibling species introgression also stresses the relative stability of the local deme in spite of the infusion of foreign genes.

VI. ACKNOWLEDGMENTS

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VII. REFERENCES

- BAMS, R. A. 1976. Survival and propensity for homing as affected by presence or absence of locally adapted paternal genes in two transplanted populations of pink salmon (*Oncorhynchus gorbuscha*). *J. Fish. Res. Board Can.* 33(12): 2716—2725.
- BERTSSON, K.-E. and R. JOHANSSON. 1977. Havsöringundersökningar i Anråsån. *Medd. Havsfiskelab., Lysekil* 230. 20 p. (In Swedish.)
- BERTMAR, G. 1979. Home range, migrations and orientation mechanisms of the Indalsälven trout, *Salmo trutta* L. *Rep. Inst. Freshw. Res., Drottningholm* 58: 5—26.
- CARLIN, B. 1965. Märkning av odlade havsöringsungar i utvandringsfärdig storlek. *Svensk Fisk. Tidskr.* 74(7/8): 97—101. (In Swedish.), *Salm. Res. Inst. LFI Medd.* 1/1965, Bilaga 7. 11 p. (In Swedish with English abstract.)
- CLAYTON, J. W. 1981. The stock concept and the uncoupling of organismal and molecular evolution. *Can. J. Fish. Aquat. Sci.* 38(12): 1515—1522.
- DiMICHELE, L. and D. A. POWERS. 1982. Physiological basis for swimming endurance differences between LDH-B genotypes of *Fundulus heteroclitus*. *Science* 216(4549): 1014—1016.
- EHNBO, N. 1966. Lax och laxöring i Nybroån. *Svensk Fisk. Tidskr.* 75(11/12): 180—181. (In Swedish.)
- GÖNCZI, A. 1965. Sammanfattning över försök med märkning av regnbåglax vid västkusten 1962. *Svensk Fisk. Tidskr.* 74(1/2): 6—7. (In Swedish.)
- HORRALL, R. M. 1981. Behavioral stock-isolating mechanisms in Great Lakes' fishes with special reference to homing and site imprinting. *Can. J. Fish. Aquat. Sci.* 38(12): 1481—1496.
- LARSSON, P.-O., N. G. STEFFNER, H.-O. LARSSON and C. ERIKSSON. 1979. Review of Swedish sea trout (*Salmo trutta* L.) stocks based on results of tagging experiments. *Salm. Res. Inst. Rep.* (2). 31 p. (In Swedish with English abstract.)
- LEGGETT, W. C. 1977. The ecology of fish migrations. *Ann. Res. Ecol. Syst.* 8: 285—308.
- LINDQUIST, A. 1958. Fischereibiologische Untersuchungen an der Meerforelle in der Provinz Bohuslän (Schweden). *Rep. Inst. Mar. Res., Lysekil. Ser. Biol.* 9. 23 p.
- LLOYD, L. 1854. Scandinavian adventures. Vol. I. Rich. Bentley, London. 512 p.
- NALL, H. 1930. The life of the sea trout. Seeley, Serv. & Co. Ltd, London. 335 p.
- NYMAN, L., J. HAMMAR and R. GYDEMO. 1981. The systematics and biology of landlocked populations of Arctic char from Northern Europe. *Rep. Inst. Freshw. Res., Drottningholm* 59: 128—141.

- PUKE, C. and N. STEFFNER. 1964. Försöksutsättning av havsöring i Dalälvens mynning. *Svensk Fisk. Tidskr.* 73(5/6): 65—68. (In Swedish.)
- RICKER, W. 1972. Heredity and environmental factors affecting certain salmonid populations. p. 19—160. In *The stock concept in Pacific salmon*. Eds.: R. C. Simon and P. A. Larkin. McMillan Lectures in Fisheries. Univ. B. C., Vancouver.
- ROS, T. 1966. Gullspångslaxen — en svensk praktfisk för fiskevården. *Svensk Fisk. Tidskr.* 75(11/12): 162—166. (In Swedish.)
- RUNNSTRÖM, S. 1940. Vänerlaxens ålder och tillväxt. *Rep. Inst. Freshw. Res., Drottningholm* 18. 38 p. (In Swedish with English summary.)
- RYMAN, N., F. W. ALLENDORF and G. STÅHL. 1979. Reproductive isolation with little genetic divergence in sympatric populations of brown trout (*Salmo trutta*). *Genetics* 92: 247—262.
- and G. STÅHL. 1981. Genetic perspectives of the identification and conservation of Scandinavian stocks of fish. *Can. J. Fish. Aquat. Sci.* 38(12): 1562—1575.
- STEFFNER, N. G. 1975. Rapport från fiskeristyrelsens fiskodlingsgrupp. *Inform. Inst. Freshw. Res., Drottningholm* (3). 13 p. (In Swedish.)
- SVÄRDSON, G. 1966. Öringen. *Fiske* 66: 2—31. (In Swedish.)
- 1967. Lax och öring i Em. *Inform. Inst. Freshw. Res., Drottningholm* (7). 47 p. (In Swedish.)
- 1979. Speciation of Scandinavian *Coregonus*. *Rep. Inst. Freshw. Res., Drottningholm*. 57. 95 p.
- and H. ANHEDEN. 1963 a. Långvandrande skånsk havsöring. *Svensk. Fisk. Tidskr.* 72(8/9): 109—113. (In Swedish.)
- and H. ANHEDEN. 1963 b. Könkvot och utvandring hos Verkeåns öring. *Svensk Fisk. Tidskr.* 72(12): 165—169. (In Swedish.)
- and N.-A. NILSSON. 1965. Öring som sättfisk. Handboken Vattenkraft-Fiske 22. (Mimeographed in Swedish.)
- and G. MOLIN. 1981. The impact of eutrophication and climate on a warmwater fish community. *Rep. Inst. Freshw. Res., Drottningholm* 59: 142—151.
- TOIVONEN, J. and A. TUHKUNEN. 1975. Migration of sea trout along the coastal waters of Finland on the basis of tagging experiments. *MS. Int. Council Explor. Sea. CM* 1975/M: 3. 13 p.
- WADDINGTON, C. H. 1942. Canalization of development and the inheritance of acquired characters. *Nature* 150: 563—564.
- 1953. Genetic assimilation of an acquired character. *Evolution* 7: 118—126.
- 1957. The strategy of the genes. Allen and Unwin, London. 262 p.
- WESSEL, L. 1971. Havsströmmar. Instruktion för stridstjänster vid flottan, Ubåtsjakt, Hydrografi. Bil. 4: 7—9. (In Swedish.)
- WICKSTRÖM, H. 1974. Smolt taggings in Lake Vänern 1960—69. *Inform. Inst. Freshw. Res., Drottningholm* (9). 68 p. (In Swedish with English summary.)
- ZARNECKI, S. 1963. Differentiation of Atlantic salmon (*Salmo salar* L.) and of sea trout (*Salmo trutta* L.) from the Wisła (Vistula) river into seasonal populations. *Acta Hydrobiol.* 5(fasc. 2/3): 255—294.

Ultrasonic Tracking of Atlantic Salmon (*Salmo salar* L.) – I. Movements in Coastal Regions

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ABSTRACT

Atlantic salmon have been tracked using ultrasonic transmitters in the archipelago and estuary of the presumed home river during their spawning migration. 21 trackings were made off the River Lule in the Bothnian Gulf, 7 off the River Klarälven in Lake Vänern. Tracking times ranged up to 40 hours (mean 16 hours) and the tracking distance was up to 60 km (mean 19 km).

Approximately 60 % of the trackings which lasted for more than 5 hours showed erratic movements, statistically not significantly different from random walk. For this group the net progress was slow (typically 10 km/day) and the resulting direction could be both towards and away from the river. All these erratic tracks were observed in the river estuary or in the innermost archipelago. The behaviour is similar to that seen during the riverine phase of the migration. A high incidence of retrograde movements in one branch of the Lule estuary seems to be caused by pollution.

The lesser group with a significant degree of oriented movement showed a net progress of approximately 25 km/day. In three cases, when recaptures made the river affiliation known or probable, the migration direction was towards the home river. The remaining 5 trackings show a direction away from the presumed home river.

The observed cruising speed was in the range 0.5–1.0 body length/s. This speed is close to what theoretically would give a minimum energy consumption per unit distance travelled. Possible orientation cues are discussed and an experiment which shows that a salmon was sensitive to the presence of a weak magnetic field is presented.

On numerous occasions the salmon were observed to detect and avoid traps and set nets. Detection was at approximately 10 m distance and seemed to be non-visual. A strong cooperation between different traps was noted. This means that a small increase in the number of salmon traps in the archipelago can have a considerable effect on the proportion of the total run which is caught in the river.

Observations on swimming depth and behaviour in relation to the hydrography are discussed in an accompanying article.

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and discussed for example by HASLER (1966), HARDEN—JONES (1968) and STASKO *et al.* (1973). The return to the spawning grounds can be divided in three phases: an ocean phase from the distant feeding areas to the generalized region of the home river, a slower coastal phase in which the river mouth is approached, and a final stream phase where olfaction and rheotaxis guide the salmon to the parent tributaries and spawning redds.

In 1976 adult salmon (*Salmo salar*) were tracked in the estuary of the River Lule in the northern Bothnian Gulf. The study was continued in 1978, when the trackings were made in the archipelago at a greater distance from the river. Additional experiments were made in Lake Vänern during 1979 and 1980.

I. INTRODUCTION

The anadromous migration cycle of the salmon species, and the remarkable homing to the river of birth, is well known and has been reviewed

The main objective of the studies was to investigate the behaviour of salmon in relation to hydrography, as a background for the assessment of the effects of cooling water discharges on salmon migration.

Several other telemetry experiments have been made during the coastal approach of salmonid species: On Atlantic salmon (*Salmo salar*); WAATEVIK 1980 and SMITH *et al.* 1981, on sockeye salmon (*Oncorhynchus nerka*); MADISON *et al.* 1972, GROOT *et al.* 1975 and STASKO *et al.* 1976, and finally on pink salmon (*Oncorhynchus gorbuscha*); STASKO *et al.* 1973.

All the studies, except that of WAATEVIK 1980 were made in areas with a strong tidal influence. In common to the observations are large variations between the tracks of individuals, complex paths and on occasion a progress away from the presumed home river. When trackings were made in estuaries with a strong freshwater influence, the movements of the salmon were dominated by passive advection by the tidal currents, and the net progress was slow.

The present trackings were undertaken in an environment without tidal currents and differs from earlier experiments in the absence of salinity difference, or very weak salinity gradient in the estuaries. In this way the behaviour of the salmon could be studied in relation to temperature as a single parameter.

A marked ability of the salmon to avoid fishing gears was found, and some implications of this behaviour for the effects of the fishing intensity in the archipelago are discussed.

This report will present and discuss the observed horizontal movements from all the trackings. In an accompanying article (Ultrasonic tracking of Atlantic salmon. — II. Swimming depth and temperature stratification. Referred to as B below) the swimming depth observations are presented, and an attempt is made to interpret them with a new model of olfactive orientation.

II. BACKGROUND

The River Lule

The River Lule discharges into the Bothnian Gulf in the northern Baltic (Fig. 1). Since 1971 there

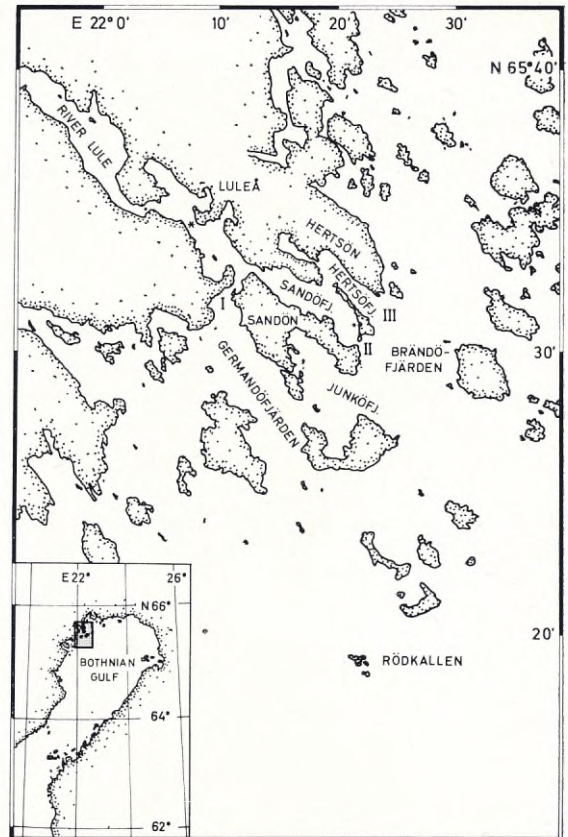


Fig. 1. The estuary and archipelago of the River Lule.

has been a power dam at the town of Boden, approximately 50 km from the river mouth. This dam is a definite blockage to the salmon migration, and the few remaining spawning grounds in the river contribute insignificantly to the recruitment of salmon. Essentially all smolts, 100,000 per year, are reared and then planted in the lower reaches of the river. The genome of the fish in this investigation is uncertain. At least 13 different stocks and several crossings, have been released in the River Lule (LARSSON *et al.* 1979). The fishery in the archipelago is done with hoop and trap nets. During the period 1976–78 the proportion of the total catch taken in the archipelago increased considerably, due to an increase in the number of nets and a transition to more efficient, large trap nets.

The water in the Bothnian Gulf is brackish, with a surface layer of the order of 10 m thick

with approximately 2 ‰ salinity and a bottom water with salinity 3–4 ‰. The circulation in the gulf is in general cyclonal, but currents in the archipelago are variable and determined by the local wind. There are no tides and the currents are weak. The hydrography of the Lule estuary is described by BROMAN (1980). In July, when the trackings were done, the river flow is approximately 500 m³/s. The freshwater outflow is divided between three branches in the river mouth. The branches are (see Fig. 1): I Tjuvholmsundet, II Klubbnäskanalen and III Hertsöfjärden. The approximate proportions of the freshwater flow are via I 15 ‰, II 35 ‰ and III 50 ‰. In the Sandöfjärden and the Hertsöfjärden there is a gradual increase of the surface salinity, due to entrainment of intruding saltwater from below, and the salinity is 1–1.5 ‰ when the outflow reaches the Brändö- and Junköfjärd. Here the riverwater spreads in irregular plumes, which are usually separated from the 2 ‰ coastal surface water by fronts extending 1–10 km from the mouths.

Lake Vänern

Vänern is a 5,600 km² lake, which holds a land-locked stock of Atlantic salmon, separated from the ocean by the land elevation since the latest glacial period. Two salmon rivers remain after the installation of hydro-electric power; the Rivers Gullspång and Klarälven. The telemetry experiments were made in the Klarälven estuary (Fig. 2). The main part of the recruitment of Klarälven salmon is by release of hatchery reared smolts.

The experiments were done in July–August, during the spawning run. At this time the lake is strongly stratified in temperature. The hydrography of Lake Vänern and the Klarälven estuary is discussed by LINDELL 1978 and HOLMSTRÖM and CARLSSON 1978. The main branches of the River Klarälven discharge into Säterholmsfjärden and the flow of river water is approximately 150 m³/s. In Säterholmsfjärden there is a mixing with surface lake water and the plume of river water is usually concentrated along the western shore. In contrast to the situation in an estuary with salinity stratification the plume of river water can sink if the coastal surface water is warmer than the

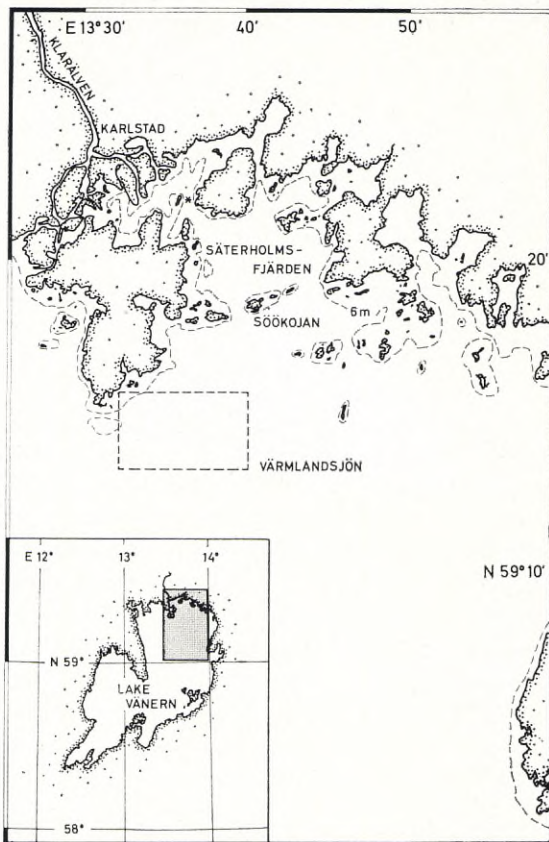


Fig. 2. The estuary and archipelago of the River Klarälven.

plume. The currents in Lake Värmlandssjön, the open basin south of the archipelago, are governed by the local wind. In the summer there is typically a weak counter-clockwise circulation, with currents of the order of magnitude 10 cm/s.

III. MATERIAL AND METHODS

Telemetry equipment

Tracking was done with a hydrophone mounted on the gunwale of the boat. The hydrophone, a Bruel & Kjaer 8101, was protected by a streamlined, flooded plastic dome, with a parabolic reflector to obtain directionality. The reflector was rotated by remote control, and the listening direction displayed on a control panel in the wheelhouse. The signal from the hydrophone was converted to audible pulses with a 50–150 kHz

Table 1. *Specifications of the ultrasonic transmitter tags.*

Type	Position or Temperature	Swimming depth
Diameter (mm)	15	15
Length (mm)	45	70
Weight in water (g)	8	13
Battery life (days)	30—60	10
Frequency (kHz)	95	95
Source strength (dB re 1 μ Pa, 1m)	145	145

tunable receiver, similar to the RC-75A receiver described by HOLLAND *et al.* 1974. Data on the ultrasonic transmitters used in the experiments are summarized in Table 1. The electronics of the position and temperature tags is described by BJÖRK 1977. Details of the depth-sensing transmitter are given in B.

Handling of fish

All fish for the experiments were caught in trap or fyke nets. In general the nets were examined every second day. When possible, arrangements were made with the fishermen to search the net an additional time, so that the salmon used in the trackings would have spent a maximum of only 24 hours in the trap. The fish which were chosen were transferred from the trap to a 40 l tank and sedated with 20 ppm MS 222, replaced from 1978 with benzocaine of the same strength. When the salmon showed signs of losing the righting reflex (after 2—5 minutes), the head was raised out of the water, and the transmitter guided down the oesophagus with a smooth inserter. A Carlin tag was fastened at the base of the dorsal fin for external identification. The water in the tank was changed and the salmon observed for a few minutes. Recovery from the light anesthesia was normally instantaneous in the fresh water. Sex was determined and the weight estimated.

All individuals were released close to the net where they had been caught — usually approximately 50 m from the outermost part of the net. The whole operation, from recovery from the trap to release, lasted less than 20 minutes. The fish were out of the water for less than one minute.

During the experiments in 1980 the surface

water temperature was 20—22°C, and the stress on the fish proved to be too great when they were handled at this temperature. Instead they were taken from the trap net to a 1 m³ holding tank, containing cool water pumped from below the thermocline. After an acclimatization period of a few hours the tagging was done as described above. The salmon were then kept for observation in the holding tank for some hours more. In some of these experiments the release was effected in positions other than at the net where the salmon had been caught.

Tracking procedure

In 1976 a 7 m open motorboat was used for tracking. The position of the salmon was determined at 10—30 minutes' intervals, by manoeuvring close to the salmon and taking bearings on points on the shore with a handheld compass. This was sometimes made from two points to get a cross bearing on the fish, but in the majority of cases, when the fish was moving, the distance and direction of the fish was estimated and position determined from a single point. The accuracy of the positions was generally good, when the salmon moved close to the shore, approximately 50 m including the uncertainty in distance between boat and fish. When the distance from the shore increased the uncertainty of position also increased. The estimated uncertainty is 100—300 m at distances greater than 1 km from land.

In 1978 and later tracking was undertaken from a 10 m boat equipped with radar. Visual bearings were still used close to land, but at greater distances radar was used for positioning, giving a maximum probable error in position of approximately 200 m. During the intervals between position fixes the boat drifted within hearing range of the transmitter, but at some distance to minimize disturbance. The approaches were made from varying directions to avoid chasing the salmon in a systematic way.

All times are given as local time (GMT — 1 hour for the experiments 1976, 1978 and 1979, GMT — 2 hours in 1980).

Data analysis

The positions were plotted on navigational charts, using the largest available scale (in the Lule

estuary 1 : 20,000, in the outer archipelago 1 : 50,000 and in Lake Vänern 1 : 60,000). From these plots the hourly positions were interpolated and the hourly net ground speeds and directions measured. The total length of the trajectory was measured along the detailed path. A schematic diagram and explanations of the parameters which were measured on the trajectory are given in Fig. 3. The movement patterns shown by several position fixes, which means timescales of the order of one hour or longer, have been classified into four main categories: passivity, intermittent movements, milling movements and directional movements. In most cases there is a distinct transition between periods of behaviour of the different categories, but the division is empirical and sometimes observed movements are intermediate and the categorization subjective.

A precise description of what is meant by the movement patterns is as follows:

- 1) Passivity: Holding position at the bottom or drifting passively in midwater over an extended period, arbitrarily chosen as one longer than 30 minutes.
- 2) Intermittent movements: Short intervals of active swimming, alternating with drift or position holding. Typically the active intervals last 10—30 minutes (displacement 100—500 m) and the passivity similar lengths of time. The tracks during swimming seem relatively straight, but direction changes between active periods can be large.
- 3) Milling movements: Swimming is nearly continuous. Frequent considerable ($> 90^\circ$) direction changes or circling.
- 4) Directional movements: Swimming is continuous for periods of longer than 1 hour. Swimming direction varying slowly ($< 45^\circ$ from one hour to the next in open water, can be greater if the movement is along a shoreline).

Without a model of the orientation process there is no statistical method that can be used to determine whether a single trajectory is the result of active orientation or not. A tentative categorization into apparently orientated and random tracks has been made with three simple nonparametric tests, presented in Fig. 3. A detailed description of the tests is given in BATSCHLET 1972. The

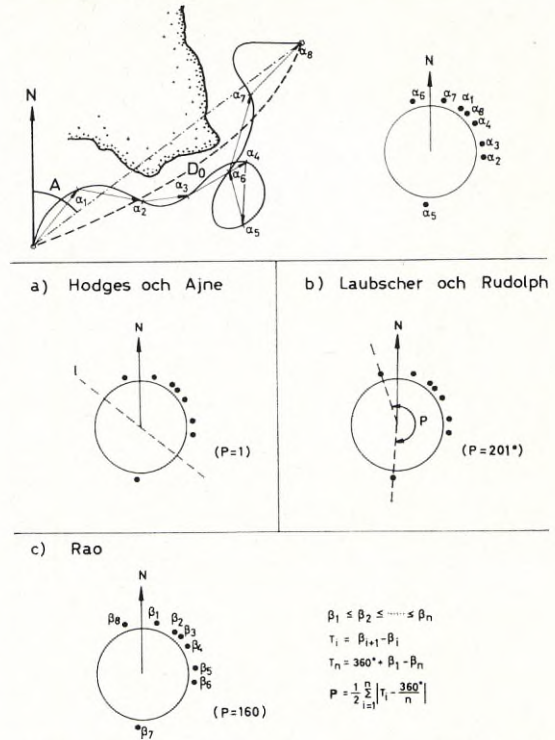


Fig. 3. Definition sketch for the analysis of the trajectories. Successive positions with a constant time interval of 1 hour were interpolated. The vectors connect these points. The hourly mean speeds and directions are given by these vectors. The total length of the trajectory, D , was measured along the actual track, and the shortest water route, D_0 , was estimated as shown in the figure.

The circular distribution of the hourly directions were constructed and used for the statistical tests a—c. In a) the test statistic, P , is the minimum number of points on one side of a diameter 1. The test statistic in b) is the smallest angle that contains all the sample points. The test c) is one which is powerful even in situations where the theoretical distribution is multimodal. The definition of the test statistic is shown in the figure.

null hypothesis is that the salmon at intervals chooses new swimming directions at random, and that these directions have a uniform circular distribution. With the assumptions that the choices are made at time intervals shorter than one hour, and that advection and constraints from the shores can be neglected, the observed hourly directions will be random if the null hypothesis holds.

Experimental artifacts

As discussed above the fish were approached from various directions during the tracking, but no

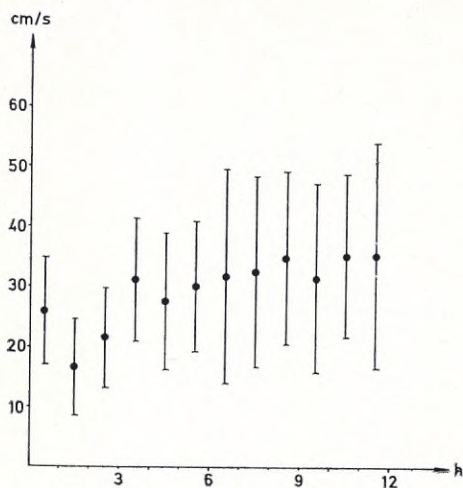


Fig. 4. The ensemble average and standard deviation of the hourly mean swimming speeds as a function of time after release. The average is for all experiments in 1976 and 1978, excluding D, F, J76 and D78.

evident changes of swimming direction were associated with the manoeuvres of the tracking boat. Occasionally the boat was deliberately steered over a salmon equipped with a depth sensitive tag. When the boat was directly above the fish, and it could be seen on the echograph, it dived to approximately 10 m. Within a few minutes the salmon had resumed the earlier swimming depth, and continued on the same heading as before.

The salmon seemed to tolerate the transmitter well. In 1976 five of the fish were caught at the salmon hatchery in Boden, where they were kept in basins together with other adult salmon until they were stripped, 3–4 months after the tagging. Two of them died during this period due to UDN, which was in proportion to the total loss from this disease in 1976. No anomalous behaviour was observed, all fish retained the transmitter and no internal damages were detected on dissection after stripping. The only comparison which can be done to assess prolonged effects of tracking on migratory behaviour is with the results of tagging experiments. In 1978 tagging of salmon was done in the Lule archipelago simultaneous to the telemetry experiments. The recaptures show no large differences in distribution pattern and migration speed, compared to that found in salmon with

ultrasonic transmitters. The conclusion is that the transmitter *per se* does not seem to disturb the salmon, but the capture and handling is common to both techniques and effects of these can not be excluded. A transitory effect of the handling can be seen when the net hourly speeds are ordered as a function of time since release. Fig. 4 shows the mean of experiments in 1976 and 1978. There is a clear decrease during the first three hours, which is probably a reaction to the tagging or sedation. When possible the discussion of results is based on observations made later than 3 hours after the release.

IV. RESULTS

The different tracking experiments are referred to by consecutive letters, followed by the year of the experiment. In Table 2 data on the salmon and trackings are summarized. In all 28 trackings were undertaken, and the trajectories are shown in Figs. 5–6. The tracks in the inner Lule archipelago were in many cases highly irregular and a smoothing has been done to fit the scale of the figures. In Fig. 7 time series of the four movement patterns, defined in section III, are given for all experiments except F and J 76, where contact was lost almost immediately, and D 78 and A 79 where the salmon did not move from the point of release. The relative proportions of time spent on the different behaviours are summarized in Table 3.

Experiments B and C 80 deviate from the other trackings in that the salmon were manipulated to examine possible orientation cues. Salmon B 80 was deprived of the sense of smell by cutting the olfactory tracts, and C 80 was equipped with an external electromagnet. Data from these experiments are included in tables and diagrams of results, but they are excluded from the general discussion of the trackings. The observations in experiment B 80 will be discussed in B and the findings of C 80 are given as an appendix.

Tagging returns

All salmon which were tracked in the Lule area were tagged externally, and a total of 16 (76 %) have been captured and reported. The recapture data are given in Table 4.

Table 2. Individual statistics of the salmon trackings.

Exp	Salmon		Release tracking					Type of transmitter
	Length (cm)	Weight (kg)	Sex	Date	Time	T Duration (hours)	S Length (km)	
A 76		7		760707	11.00	34.0	23.2	P
B	65 ¹	4.5/4.0 ²	♂+♀	10	12.10	40.8	42.2	P
C		6/6.4 ¹		12	17.30	6.7	16.6	P
D		7		13	18.50	13.1	13.7	P
E		7/7.1 ²		14	17.45	16.9	28.5	P
F		4.5		17	16.45	0.6	0.4	P
G		5		19	10.10	10.6	10.6	P
H		6		20	16.30	16.3	21.0	P
I	75	4.5		22	09.00	27.2	25.1	P
J	60	5.5		27	09.05	1.0	2.4	T
K	115	17.0		27	17.45	13.3	20.3	T
L	65	3/3.2		29	18.15	4.8	8.6	T
A 78	90	7			780705	14.50	6.2	10.7
B	92	7	♂+♀	08	18.15	11.3	19.8	P
C	/78 ¹	6/5.8 ¹		11	09.40	15.8	29.6	P
D	98/90 ¹	10/9.5 ¹		16	18.25	5.6	0	D
E	85	6		19	17.00	34.5	58.0	D
F	75/78 ¹	5		22	17.00	30.5	32.6 ³	D
G	83	6		25	10.50	3.7	5.3	P
H	70/68 ¹	3.5/3.7 ¹		26	16.00	3.9	3.9	P
I	75	5		27	20.25	16.5	28.6	D
A 79	95	7			790822	09.30	34.0	0
B	65	5	♀	23	11.10	7.8	14.3	D
C		3		30	08.30	20.0	36.1	D+T
A 80		4		800731	07.30	10.5	8.0	D
B		3.5	♂+♀	0801	07.40	31.3	15.3	D
C		2.5		03	16.05	12.9	18.4	P
D		6		04	17.35	23.9	31.2	D

¹ measured after recapture.

² measured after recapture, gutted weight.

³ trajectory not complete.

Simultaneous with the telemetry experiments in 1978, 208 adult salmon were tagged and released in the archipelago of Lule. Preliminary results of the recaptures are as follows (MATS LARSSON pers. comm.). Of the total number released 63 % have been recaptured and reported. 78 % of the recaptures were in the Lule river or archipelago. The remaining 22 % were caught off rivers to the south of the city of Luleå (11 %) and to the north or on the eastern side of the Bothnian Gulf (11 %). This compares well with the corresponding results of the salmon tagged in connection with the telemetry experiments: 75 % of the recaptures in the Lule river and archipelago, 19 % to the south and 6 % to the north of Luleå.

The small samples and large individual variations make comparisons of travel times difficult. The largest groups with a common destination are the salmon caught in the Lule river. Among the telemetry salmon 8 were recorded in the river, all in 1976 and all released in the estuary. Travel times were in the range of 3–14 days, mean 8 days. In the 1978 tagging experiment, 12 were caught in the Lule river after 3–47 days, mean travel time 21 days. These were released in the archipelago and the larger mean travel time could be due to the greater distance. In a smaller group caught in the Pite archipelago the mean travel time is somewhat longer for the telemetry salmon (6, 10 and 30 days) than for the 8 recaptures in the

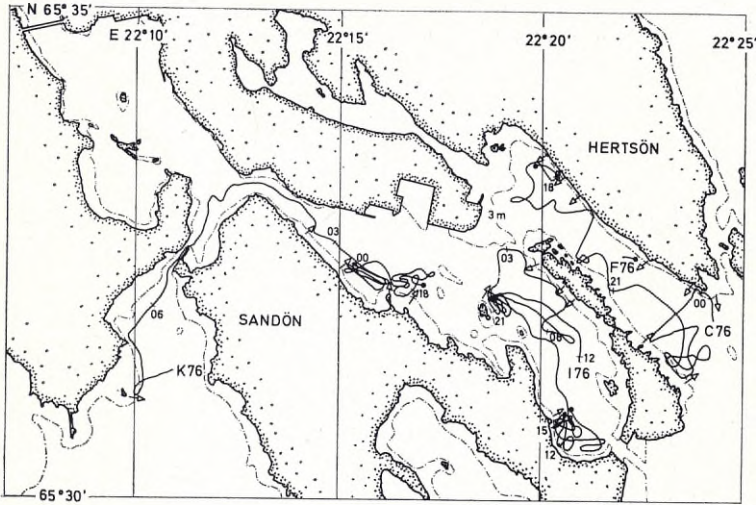


Fig. 5 a.

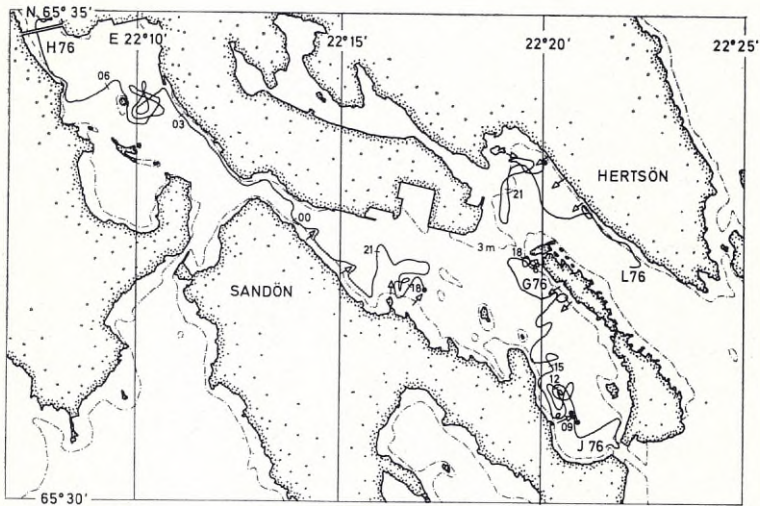


Fig. 5 b.

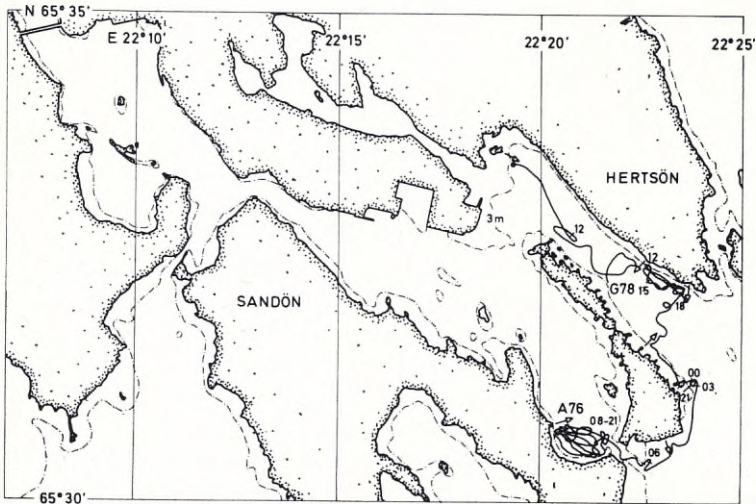


Fig. 5 c.

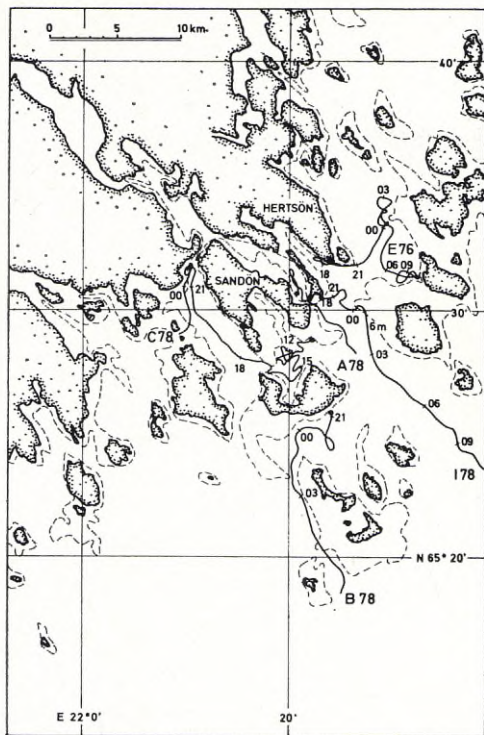


Fig. 5 d.

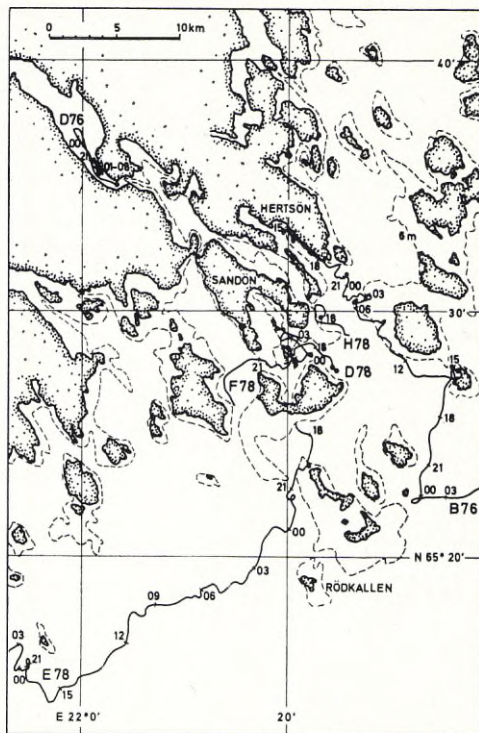


Fig. 5 e.

Fig. 5 a—e. Observed trajectories of salmon in the Lule estuary and archipelago. The point of release is marked with a filled circle. Local time is indicated at 3 hour intervals and the experiments are identified by their name at the end of the track. In a—c the positions of salmon traps are marked with a triangle and a line which shows the direction of the lead.

tagging experiment. The latter ranged between 3 and 14 days with a mean of 7 days. In neither case are the differences statistically significant.

Swimming speed

Different measures of the observed ground speed are summarized in Table 5. No current measurements were taken during tracking, so the advective part cannot be separated from the active movement of the fish. The currents, both in the Lule archipelago and in Lake Vänern, are weak, of the order 10 cm/s or less, and variable with depth. Therefore, if the salmon showed some period with directional, continuous swimming, the maximum hourly mean speed could be used as an estimate of sustained swimming speed. C, G, L 76 and G, H 78 did not have any directional period, and in these cases the hourly net displacement will

underestimate the swimming speed. If we exclude these experiments it can be seen that the swimming speeds vary between 32—136 cm/s, with 80 % falling in the range 40—80 cm/s, corresponding to approximately 0.5—1 body length/s. The average speed along the whole trajectory (U), is somewhat lower than the sustained swimming speed, and determined essentially by the proportion of passivity or intermittent movements. The mean velocity based on the shortest water distance for the whole track (U_0) is in general low, and comparable to the current velocities or the speed calculated from the time and distance between release and recapture.

Diel rhythm

In Fig. 7 the period between sunset and sunrise is indicated for each experiment. At the latitude of Luleå during July there is no real darkness. The

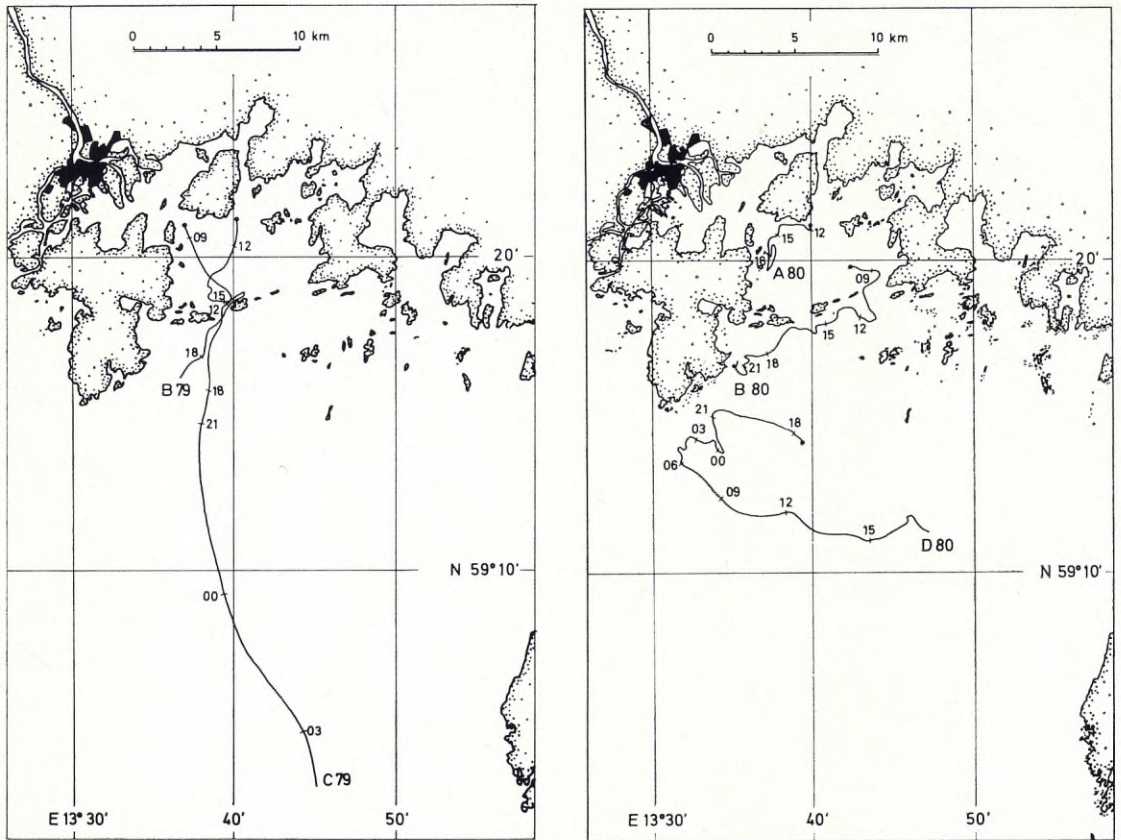


Fig. 6 a—b. Trajectories for the tracking in Lake Vänern. Notation as in Fig. 5.

minimum daylight irradiance at the surface is approximately 100 lux in the beginning of the month, decreasing to 10 lux at the end.

In a number of cases a period of passivity or intermittent movement starts just after sunset (A, B, D, I 76, E, F 78, B 80) or changes to milling or directional movement just before sunrise (B, E, H, I 76, E, F, I 78). A calculation was made of the average relative proportion of time when the salmon were classified as passive for all experiments with a total tracking time of more than 10 hours. For the period between sunset and sunrise this gave 32 % compared to 15 % for the tracking time while the sun was up. This increase of passivity can also be seen in Fig. 8, which shows the distribution of movement patterns as a function of local time for the trackings in Luleå. The sun is at its lowest point approximately 20 minutes before midnight local time in Luleå. There were

several individuals which deviated from this activity pattern, for example E 76 and C 79 which swam actively and directionally during most of the night.

Orientation

The geographic direction from the point of release to the position where tracking was terminated is given in Table 6. A measure of the straightness of the observed path is the straightness index, SI, introduced by STASKO *et al.* 1973 and defined as the ratio of the shortest water distance, start to end of track, to the length of the fish's path. In Table 6, SI is compared with the results of the nonparametric tests for a deviation from randomness in choice of direction. It is seen that for the present trackings $SI=0.5$ can be used as a critical value. If $SI > 0.5$ then the trajectory deviates significantly from randomness.

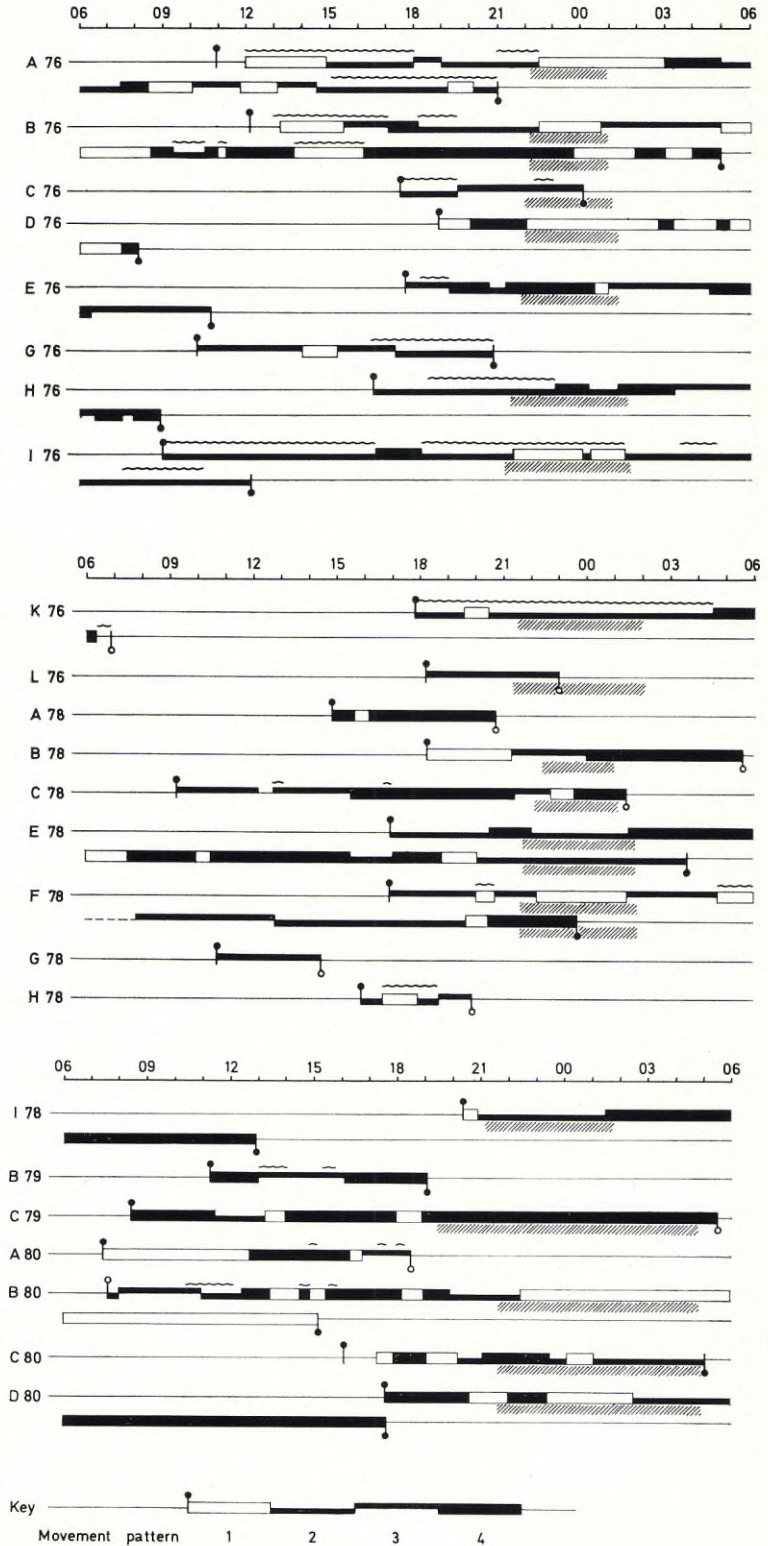


Fig. 7. Time-series of the activity patterns of the individual salmon. 1 — passivity, 2 — intermittent movement, 3 — milling movement, 4 — directional movement. The start and end of tracking is indicated with a circle above and below the baseline. The period between sunset and sunrise is shown by a streaked band. Periods when the behaviour of the salmon was influenced by the presence of fishing gears are indicated by an undulating line above the baseline.

Table 3. Percentage of total observation time (excluding first 3 hours of each experiment), when the salmon's behaviour was classified as; 1 — passive, 2 — intermittent movement, 3 — milling movement, 4 — directional movement. N is the percentage of time when the behaviour was influenced by the presence of fishing gear.

Exp	Behaviour, % of total time					Hours
	1	2	3	4	N	
A 76	30	47	13	10	37	31.3
B	32	14	15	38	19	38.2
D	83	0	0	17	0	10.3
E	4	4	56	37	0	14.2
G	16	47	38	0	57	7.7
H	0	34	27	40	26	13.4
I	15	78	0	7	66	24.4
K	0	80	0	20	84	9.8
B 78	0	0	33	67	0	8.3
C	7	0	31	62	5	12.8
E	10	41	0	48	0	32.0
F	22	25	42	11	8	28.0
I	0	15	0	85	0	13.7
A 79	100	0	0	0	0	30.7
C	10	7	0	83	0	17.7
A 80	33	0	22	44	9	8.1
B	67	14	1	18	6	28.8
C	20	56	0	24	0	9.9
D	21	17	0	63	0	21.1

Table 4. Recaptures of salmon released in the telemetry experiments 1976 and 1978.

Exp	Region of capture	Days since release	Distance (km)
A 76	LR	13	53
B	P	10	60
C	LR	14	47
D	LR	5	33
E	LO	79	10
F	LR	9	52
G	LR	8	51
H	LR	6	48
I	LR	3	32
J	LE	2	3
L	LR	8	38
C 78	LO	7	14
D	P	30	47
E	P	6	52
F	K	9	55
H	LO	10	19

LR — Lule River
 LE — Lule estuary
 LO — Lule outer archipelago
 P — Pite archipelago
 K — Kalix archipelago

Table 5. Observed ground speeds in the individual trackings. U — mean speed along observed trajectory, U_0 — mean speed along shortest water route, U_{max} — maximum speed observed over a 1 hour interval. All speeds in cm/s.

Exp	U	U_0	U_{max}	Release — recapture
A 76	19	5	32	5
B	29	15	69	7
C	69	19	51	4
D	29	4	67	8
E	47	12	57	0.1
F	—	—	—	7
G	28	9	21	7
H	36	18	40	9
I	26	1	46	12
J	—	—	—	2
K	42	17	83	—
L	50	15	53	6
A 78	48	27	66	—
B	49	35	111	—
C	52	18	71	2
D	—	—	—	2
E	47	23	76	10
F	32	8	76	7
G	40	18	39	—
H	28	11	31	2
I	48	35	57	—
A 79	—	—	—	—
B	51	36	60	—
C	50	47	136	—
A 80	21	8	49	—
B	14	8	46	—
C	40	7	66	—
D	36	11	54	—

In an archipelago with straits and bays there are many restraints on the possible migration directions. Disregarding these complications a hypothetical 'appropriate direction' was determined for each point of release. In the Lule experiments the direction towards the sound at Bergnäset (marked with an asterisk in Fig. 1) was chosen. In Lake Vänern the direction to the strait at Mårholmen (marked similarly in Fig. 2) was taken as the expected direction. In Fig. 9 the deviations of the observed directions from the 'appropriate' ones are given as vectors, with SI as the length.

Response to nets

On more than 100 occasions the salmon were in close contact with salmon fyke or trap nets, and

in Lake Vänern set nets. None of these approaches led to the capture of the salmon. Three typical behaviour sequences could be seen on the approach to the lead of a salmon fyke or trap net.

- a) The salmon turned immediately towards deep water, rounded the heart and trap and continued along the shoreline, moving back into more shallow water. This avoidance manoeuvre was completed within a few minutes, and details could not be observed.
- b) The salmon began by swimming back and forth along the leader, occasionally stopping for periods of 5–10 minutes. In cases when the distance from the leader could be estimated it was typically 5–15 m. This pacing along the

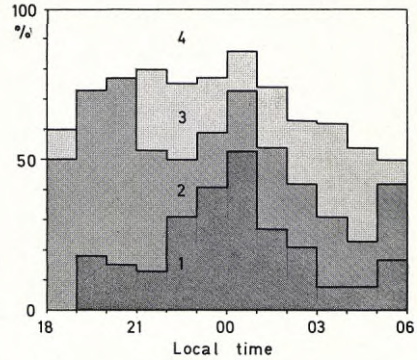


Fig. 8. Relative frequency distribution of observed movement patterns; 1 — passivity, 2 — intermittent movement, 3 — milling movement, 4 — directional movement. Average of all experiments 1978 and 1979, the first 3 h of tracking are excluded.

Table 6. Net movement direction, (*A*), and straightness index (*SI* — defined as the ratio Do/D , see Fig. 3). Results of the non-parametric tests for randomness of the trajectory.

Exp	A (deg)	SI	Significance level, test according to:		
			Rao	Laubscher and Rudolph	Hodges and Anje
A 76	227	0.24	—	—	—
B	146	0.52	++	+	+++
C	132	0.27	—	—	—
D	315	0.14	—	—	—
E	97	0.26	—	—	—
G	345	0.33	—	—	—
H	306	0.51	+++	++	+++
I	350	0.04	—	—	—
J		0.39			
K	251	0.41	—	—	—
L	136	0.30			
A 78	143	0.57	++	—	—
B	176	0.72	+++	+++	+
C	273	0.35	—	—	—
E	235	0.50	++	++	++
F	249	0.26	—	—	—
G	146	0.45	—	—	—
H	130	0.41	—	—	—
I	136	0.73	+++	+++	+++
B 79	192	0.72	+++	++	—
C	172	0.94	+++	+++	+++
A 80	242	0.37	—	—	—
B	230	0.60	++	++	—
C	245	0.17	—	—	—
D	125	0.29	—	++	—

— no significant deviation from random track.
 + deviation significant at 10 % level.
 ++ deviation significant at 5 % level.
 +++ deviation significant at 1 % level.

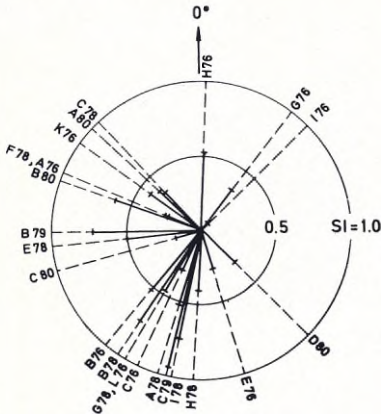


Fig. 9. Polar diagram of the observed directions, start to end of track, relative to the expected migration direction from the position of release. The magnitude of the straightness index SI is shown by the length of the solid line.

leader ended with the salmon rounding the heart as in a), 10 to 60 minutes after arrival at the net.

- c) The salmon stopped and began drifting back from the net. This drift was sometimes interrupted by the leader of a trap downstream, or a constriction such as the Klubbnäas channel, which induced active upstream movement back to the net. This sequence could be repeated several times. Alternatively the salmon stopped and stayed holding position for a relatively long time, up to several hours, before starting out on some direction away from the net, milling in a large area downstream from the trap.

The same individual could alternate between the different types of avoidance on the approach of different nets, and the same net was avoided in different ways by different salmon.

In Fig. 7, periods when the behaviour was influenced by the presence of fishing gear are indicated. These periods correspond to avoidances of type b or c. Several examples of net avoidance can be seen in Fig. 5 a—c.

Response to dredging

In 1976 intense dredging work was in progress. The channel at Klubbnäset was widened and dredged sand was dumped on the southeast tip of Svartö.

A, I and J 76 were all tracked during approaches to dredgers in operation. The salmon came to within 150–100 m distance without any avoidance reaction. At closer range contact with the transmitter was lost in the intense noise from the dredger, but the salmon passed without any appreciable delay, and seemed essentially unaffected by the dredging at even closer range.

DISCUSSION

Migration speed and direction

Based on the straightness index the tracking can be divided into two groups; one with predominantly erratic movements and slow net progress and one where the trajectory deviates significantly from random walk. The former group is the larger one and is chosen as those with SI 0,5. If we exclude trackings lasting less than 5 hours, and D 78 and A 79 where the salmon remained passive at the release position, they constitute 11 out of 19 trackings (A, C, D, E, G, I, K 76, C, F 78 and A, D 80). In this wandering and erratic group all trackings both started and ended in the inner archipelago, where the river influence is strong.

The net ground speed was slow (U_0 in the range 1–19 cm/s) and the overall progress could be both up- and downstream in the estuary. A similar slow or retrograde movement of Atlantic salmon in a river estuary has been reported in telemetry studies by ELSON *et al.* 1972 and STASKO 1975, and for sockeye salmon by GROOT *et al.* 1975. Stasko and Groot interpreted the slow progress as a general response of anadromous fish to a change from salt to fresh water, whereas ELSON described the behaviour as a response to pollution.

In the Lule estuary the seawater is hyposmotic and in Lake Vänern there is no change in salinity from lake to river water. A migration delay due to physiological adjustment seems unlikely in both cases. Pollution may well be a contributing factor to the slow progress observed in the Lule estuary. In the innermost Hertsöfjärd the effluents from a steelworks and a coke-oven plant are discharged into the surface water. During 1976 there were also large quantities of silt from dredging, which increased the turbidity in the Hertsöfjärd in

particular. It was noted that all salmon caught and released in the Hertsöfjärd moved downstream and out of the bight. In the Sandöfjärden, a branch of the estuary which is less polluted, most trackings showed an upstream, although slow, progress.

Retrograde movement in the Hertsöfjärd was observed in the first three experiments in 1976, and was the reason for the solitary release into the river, D 76. The purpose was to check whether the experimental situation caused a reversal of migration direction, and the assumption was that all movements in the river would be upstream. Initially the salmon did move upstream, but at the end of the tracking it alternated between passive drift and active movement, with no net progress. In later telemetry studies of salmon riverine movements (POWER and McCLEAVE 1980, WESTERBERG 1977) much wandering both up- and downstream has been observed. The net speeds found in these studies were generally quite low, of the order of magnitude 1 cm/s. It seems that a decrease in the progress in the estuary is the start of an equally slow riverine migration. Whether this slow progress is limited to hatchery reared stocks, with an unclear history of imprinting and a genome not adapted to the river, cannot be decided.

One obvious contribution to the delay was that the salmon were impeded by nets in the estuary. This is particularly clear in some of the trackings in the Sandöfjärd, like G, I and K 76, when the salmon spent more than half the total time milling or waiting adjacent to salmon trap nets.

8 salmon (B, H 76, A, B, E, I 78, B and C 79) have straightness index > 0.5 . In this group B, H 76 and E 78 have been recaptured. H 76, which was the only salmon tracked while entering the Lule river, was also captured in the river. B 76 and E 78 were both recaptured in the Pite river estuary. E 78 was tracked out to open water and then back into the archipelago off the Pite river and tracking of B 76 was abandoned when the salmon headed out to open water.

If the recaptures give an indication of the origin of the salmon then the migration directions of these three were towards the home stream. The relatively high proportion of strayers from other river stocks in the Lule archipelago could mean

that the direction away from the estuary was adequate for A, B and I 78 also. This explanation is, however, unlikely for the trackings in 1979. There are two salmon stocks in Lake Vänern, but the morphological differences are large and the salmon used in the experiments were typical of the Klarälven stock.

The most probable conclusion is that several of the salmon moved actively away from the home river. Tracking salmon in a Norwegian fjord WAATEVIK (1980) found that all the six salmon tracked had an initial phase of retrograde movement, lasting for up to 24 hours after release. Active retrograde movements were also observed in some of the trackings of sockeye salmon reported by STASKO *et al.* (1976). This behaviour may be part of the normal migration of salmon, akin to the temporal reversal migration in birds (EVANS 1972), or it may be an artifact caused by the experimental situation. In the latter case the retrograde movement could be a reorientation to an orientation cue which was lost during the handling prior to release. This is supported by the observation that reversals were more frequent when the salmon were caught and released in the outer archipelago, where the temporal variations of the hydrography are large, compared to releases in the estuary where the river influence is more permanent. In WAATEVIK's experiments, where all salmon showed reversal, the salmon were caught in the river and displaced approximately 10 km out in the fjord.

The average net ground speed in the group with $SI > 0.5$ was 30 cm/s, and the movement was classified as directed and continuous during approximately 60 % of the tracking time. This net speed, (26 km/day), is high compared to most speeds found in the tagging-recapture experiment of 1978. Captures in the Lule archipelago showed net speeds of less than 5 km/day and those recaptured off neighbouring rivers to the north and to the south ranged between 5 and 10 km/day. The two salmon with the greatest travel distance, caught on the Finnish side of the Bothnian Gulf, had a comparable net speed of approximately 30 km/day. In laboratory experiments maximum sustained swimming speeds of 2–3 body lengths/s have been attained for salmonids (WEBB 1975). The observed maximum swimming speeds in the

telemetry trackings are in general well below this, ranging between 40–80 cm/s or approximately 0.5–1.0 body length/s. A good agreement is, however, found with a theoretical optimal swimming speed. This is defined as the speed which uses the minimum energy cost to cover a given distance through water. With the body lengths of the salmon used in the trackings WARE's (1978) extrapolations of data for sockeye salmon have been used to calculate 45–55 cm/s as the optimal cruising speed. The increase in energy cost per unit distance is small for a moderate increase of the speed above the optimum. Hence the observed 40–80 cm/s range of cruising speed results in an energy expenditure within 10 % of the theoretical minimum.

Orientation cues

Goal orientation to the home river requires some environmental stimuli for the directional control. Several possible cues have been suggested for salmon migration; visual information in the form of celestial cues or landmarks, geomagnetic, electric and gravitational fields, acoustic signatures of shorelines or some of a large number of characteristics of the water itself (STASKO *et al.* 1973). As has been found for the navigation of migrating birds it seems probable that salmon may use a hierarchy of cues, which are redundant or complementary to each other.

That olfaction plays an essential role in salmon homing is well documented. A recent review is given by HASLER and SCHOLZ 1978 and experimental work on Baltic salmon is reported by BERTMAR and TOFT 1969. Olfactive orientation either demands that the salmon can sense the horizontal gradients of the olfactant, or that the olfactant is a release stimulus used in combination with an additional directional information. In B the observations of swimming depth and vertical stratification is used to develop a model of olfactive orientation, where the vertical gradients of the olfactant and the water current is combined to give an orientation cue for the salmon. This, or some other olfactive orientation mode, is probably the primary orientation mechanism for salmon migration in coastal water.

The increased frequency of passivity between sunset and sunrise indicates that some visual

orientation, or motivation to orient, was also involved. In most trackings the fish moved in deep water, and when the swimming depth was measured the salmon was well above the bottom. In the Lule estuary, however, the salmon sometimes followed the shoreline at a distance of less than 100 m, approximately along the 3 m isobath. Examples are B, D and H 76. In these cases a simple rheotaxis with visual contact with the bottom seems likely.

HASLER (1966) argues that a suncompass mechanism could account for the ocean phase of salmon migration. In the coastal zone the sun may still be an aid for orientation and course keeping. STASKO *et al.* (1976) reports responses to the appearance and disappearance of the sun in several sockeye salmon tracked in an archipelago. In the present trackings such changes of behaviour related to the sun were looked for, but seldom found. In one case (B 76) a change from passive drift to directed active swimming coincided with the appearance of the sun from behind the clouds. The reversed sequence was noted in two other instances, but in those cases the timing was more difficult to assess. On most occasions no change of swimming activity or direction was noted and the cases mentioned may be coincidental. Celestial cues are not obligatory for directed active movements over extended periods of time, which is seen for example in A 78, when the tracking was done in thick fog, and C 79 where the salmon swam on an essentially constant course during the whole of an overcast night.

During the tracking periods in 1976 and 1978 the rate of flow in the Lule river was constant, to within 10 % of 500 m³/s. This means that a possible influence of the river discharge on migration behaviour could not be studied. No strong correlation could be found between wind strength or direction and salmon behaviour. The range of meteorological conditions encountered during tracking is limited and the material too small to allow generalizations about effects of weather.

Geoelectric fields, generated by water moving through the geomagnetic field, has been suggested as a possible cue in salmon migration (ROMMEL and McCLEAVE 1973). The geomagnetic field itself may also be detectable, as has been shown in an increasing number of animals. Experiment C 80

was an attempt to study the importance of geomagnetism for orientation. The salmon was fitted with a coil, which was turned on and off in a 2 hour cycle, producing a magnetic field in the vicinity of the head of the salmon, with a strength of the same order of magnitude as that of the geomagnetic field. A statistical analysis of the movements shows that there was a significant correlation between the behaviour of the fish and the switching on and off of the weak magnetic field. Whether the reaction was through magnetoreception or electroreception could not be determined. The value of this solitary experiment lies mainly in the demonstration of a new technique of field experimentation with fish orientation. More trackings of a similar kind must be undertaken in order to make any generalizations about whether magnetic or electric fields are used in salmon migration. Technical details and a discussion of the experiment is given as an appendix.

Avoidance of fishing gear

Tagging returns and the net speed seen in the telemetry experiments, indicate that salmon spend roughly 10 days in the archipelago and the estuary. In the River Lule essentially all salmon entering the river are eventually caught, and during the period 1976—78 the river catch was roughly 1/3 of the total catch in the archipelago, estuary and river. In view of this it is not inconsistent that none of the salmon were caught during the 450 hours of tracking.

The salmon's means of detection of the net is unclear. On those occasions when the distance to the leader could be estimated it was of the order of 10 m when the salmon stopped or veered. The turbidity in the estuaries is high, with Secchi disc readings in the range 1—2 m, and visual detection seems improbable at this distance. Detection was effective both from the up- and the downstream side, which would exclude olfactory clues. One possible stimulus is the sounds generated by the stationary net in flowing water.

In many cases the avoidance of one net led to the encounter of another one, which the salmon would have passed clear of otherwise. This effect means that if the probability of catch is constant for a single encounter, then there is a non-linear relation between the number of traps in the area

and the accumulated risk of capture during the passage. When the density of traps increases, the number of direct encounters will increase in proportion and in addition to this, the number of secondary encounters will rise rapidly. This physical cooperation between different traps means that the proportion of the total salmon run which reaches the river can be very sensitive to the fishing pressure in the archipelago.

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The construction and maintenance of the telemetry equipment was made by LENNART BJÖRK, who has also been instrumental in both field work and data analysis. LISA LEMPERT and GÖRAN NYBERG shared with me many of the long hours at sea. MATS LARSSON and STEN ANDREASSON attended to the practical arrangements in Luleå. The typing was done by AGNETA HILDING and the charts were prepared by KRISTINA HANSSON. I would like to express my gratitude to all these people, and to the salmon fishermen in Luleå and Vänern for their help and interest.

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VII. REFERENCES

- BATSCHLET, E. 1972. Recent statistical methods for orientation data. p. 61—91. *In* Animal orientation and navigation. Eds.: S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs and R. E. Belleville. NASA SP-262.
- BERTMAR, G. and R. TOFT. 1969. Sensory mechanisms of homing in salmonid fish. I. Introductory experiments on the olfactory sense in grilse of Baltic salmon (*Salmo salar*). *Behaviour* 35 (3—4): 235—241.
- BJÖRK, L. 1977. Equipment for telemetry investigations. *Inform. Inst. Freshw. Res., Drottningholm* (16). 26 p. (In Swedish with English summary.)
- BROMAN, B. 1980. Luleå hamn — slutrapport. Resultat av ström- och skiktningmätningar i Lule skärgård 1974—1978. *SMHI Rep. Dnr 9/322*: 13. 43 p. (In Swedish.)
- ELSON, P. F., L. N. LAUZIER and V. ZITKO. 1972. A preliminary study of salmon movements in a pollu-

- ted estuary. p. 325—330. *In* Marine Pollution and Sea Life. Ed.: M. Ruivo. Fishing News (Books) Ltd.
- EVANS, P. R. 1972. Information on bird navigation obtained by British long-range radars. p. 139—150. *In* Animal orientation and navigation. Eds.: S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs and R. E. Belleville. NASA SP-262.
- GROOT, C., K. SIMPSON, I. TODD, P. D. MURRAY and G. A. BUXTON. 1975. Movements of sockeye salmon (*Oncorhynchus nerka*) in the Skeena River estuary as revealed by ultrasonic tracking. *J. Fish. Res. Board Can.* 32 (2): 233—242.
- HARDEN JONES, F. R. 1968. Fish migration. Edward Arnold Ltd, London. 325 p.
- HASLER, A. D. 1966. Underwater guideposts. University of Wisconsin Press, Madison. 155 p.
- HASLER, A. D. and A. T. SCHOLZ. 1978. Olfactory imprinting in coho salmon (*Oncorhynchus kisutch*). p. 356—369. *In* Animal migration, navigation and homing. Eds.: K. Schmidt-Koenig and W. T. Keeton. Springer-Verlag, Berlin.
- HOLAND, B., I. MOHUS and R. BERNTSEN. 1974. Fish telemetry, report 5. — Devices and results 1974 —. SINTEF Rep. (STF 48 A74049).
- HOLMSTRÖM, I. and B. CARLSSON. 1978. Hydrologi — Störvärnens hydrodynamik. p. 39—60. *In* Vätern en naturresurs. SNV Rapport. Liber Förlag. (In Swedish with English summary.)
- LARSSON, P.-O., H.-O. LARSSON and C. ERIKSSON. 1979. Review of Swedish salmon (*Salmo salar* L.) stocks based on results of tagging experiments. *Rep. Salm. Res. Inst.* (5). 28 p. (In Swedish with English abstract.)
- LINDELL, T. 1978. Hydrologi — skärgårdsområdenas hydrodynamik. p. 61—74. *In* Vätern en naturresurs. SNV Rapport. Liber Förlag. (In Swedish with English summary.)
- MADISON, D. M., R. M. HERRALL, A. B. STASKO and A. D. HASLER. 1972. Migratory movement of adult sockeye salmon (*Oncorhynchus nerka*) in coastal British Columbia as revealed by ultrasonic tracking. *J. Fish. Res. Board Can.* 29 (7): 1025—1033.
- POWER, J. H. and J. D. McCLEAVE. 1980. Riverine movements of hatchery-reared Atlantic salmon (*Salmo salar*) upon return as adults. *Env. Biol. Fish.* 5 (1): 3—13.
- ROMMEL JR. S. A. and J. D. McCLEAVE. 1973. Sensitivity of American eels (*Anguilla rostrata*) and Atlantic salmon (*Salmo salar*) to weak electric and magnetic fields. *J. Fish. Res. Board Can.* 30 (5): 657—633.
- SMITH, G. W., A. D. HAWKINS, G. G. URQUHART and W. M. SHEARER. 1981. Orientation and energetic efficiency in the offshore movements of returning Atlantic salmon (*Salmo salar* L.). *Scot. Fish. Res. Rep.* 21. 22 p.
- STASKO, A. B. 1975. Progress of migrating Atlantic salmon (*Salmo salar*) along an estuary, observed by ultrasonic tracking. *J. Fish. Biol.* 7: 329—338.
- STASKO, A. B., R. M. HERRALL, A. D. HASLER and D. STASKO. 1973. Coastal movements of mature Fraser river pink salmon (*Oncorhynchus gorbuscha*) as revealed by ultrasonic tracking. *J. Fish. Res. Board Can.* 30(9): 1309—1316.
- STASKO, A. B., R.M. HERRALL and A. D. HASLER. 1976. Coastal movements of adult Fraser River sockeye salmon (*Oncorhynchus nerka*) observed by ultrasonic tracking. *Trans. Am. Fish. Soc.* 105 (1): 64—71.
- STASKO, A. B., A. M. SUTTERLIN, S. A. ROMMEL JR. and P. F. ELSON. 1973. Migration — orientation of Atlantic salmon (*Salmo salar* L.). p. 119—137. *In* International Atlantic Salmon Symposium. Eds.: M. W. Smith and W. M. Carter. *Int. Atl. Salmon Fdn. Spec. Publ.* 4 (1).
- WAATEVIK, E. 1980. Vandringsstudier av laks (*Salmo salar* L.) i Sandsfjorden i Ryfylke ved hjelp av akustiske merker. Unpubl. thesis. Univ. Bergen. 76 p. (Mimeographed in Norwegian.)
- WARE, D. M. 1978. Bioenergetics of pelagic fish: theoretical change in swimming speed and ration with body size. *J. Fish Res. Board Can.* 35(2): 220—228.
- WEBB, P. W. 1975. Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Board Can.* 190. 159 p.
- WESTERBERG, H. 1977. Telemetriförsök med lax och laxöring i Mörrumsån 1976. *Inform. Swed. Salm. Res. Inst.* (4): 1—10. (In Swedish.)

APPENDIX:

Reactions to a Weak Magnetic Field

Material and Methods

A coil was wound from 60 μm diameter copper wire, 300 turns with 18 mm diameter. With a 5 mA DC current the magnetic field strength in the centre of the coil was approximately $1 \cdot 10^{-4}$ Tesla. The electronics to switch the coil are shown in Fig. A1. A quartz clock crystal gave a stable oscillator frequency of 32.768 kHz, which was reduced in two 2^{14} dividers (CD 4049). The result was a square-wave with 8192 s period, ± 0.16 s, with equal on and off intervals (1 h 8 min 16 s). A hexinverter (CD 4049) was used as booster to supply current to the coil. The operating life was at least 2 days, with a silver oxide battery (UCAR 544) as the power source.

The electronics and the battery were potted in urethane rubber, resulting in a 15 mm diameter

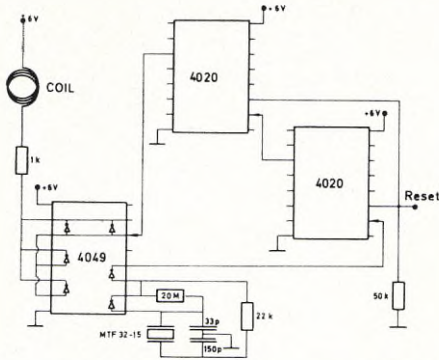


Fig. A 1. Circuit diagram of the magnetic field generator.

cylinder, approximately 60 mm long and weighing 10 g in water. Thin insulated wires connected the electronics to the coil, which was also potted in urethane rubber.

In experiment C and D 80 positions of the tracking boat were obtained by radar from another vessel drifting in the area. Position fixes were made when the tracking boat was close to the salmon, and the time between fixes was approximately 5 min during experiment C 80 and varying between 5 and 15 min in experiment D 80. The uncertainty of the radar fixes is less than 50 m, and the total maximum error in position of the fish was estimated as 100 m.

Results

A time scale was constructed from the period of the electromagnet. The full period of 8,192 s was divided by 8, giving 1,024 s, or 17 min 4 s, as a basic time interval. Starting at the onset of one magnet cycle successive points in time with this interval were calculated. The positions of the salmon at these times were interpolated from the original radar fixes. Fig. A 2 shows the trajectory of the salmon C 80 presented in this way. The times when the magnetic field change state are given in the figure. The trajectory of D 80 was treated in the same way, using the same points in time 24 hours later.

From these trajectories the mean ground speed and direction was measured for each time interval. The relative frequency distribution of the ground speed is shown in Fig. A 3. The distribution is clearly bimodal, with maxima at approximately 10 and 50 cm/s. The 10 cm/s maximum can be interpreted as time intervals when the fish was essentially immobile. The observed small displacements are due to a combination of advection by the weak currents and the uncertainty of the positions. Based on this distribution the salmon was defined as actively swimming when the measured ground speed was larger than 22.5 cm/s.

Excluding time intervals when the fish was inactive the change in observed swimming direc-

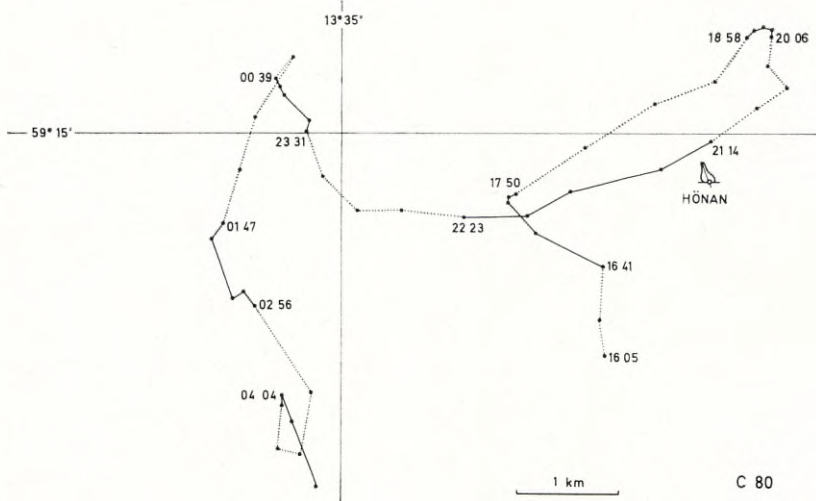


Fig. A 2. Trajectory of the salmon with electromagnet. Dotted lines shows portions of the track when the magnetic field was on. Positions with equal (1,024 s) time intervals. The location of the area shown is marked in Fig. 2.

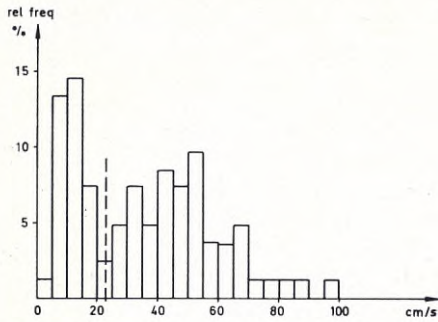


Fig. A 3. Frequency distribution of the observed ground speeds. Sum of experiments C80 and D80.

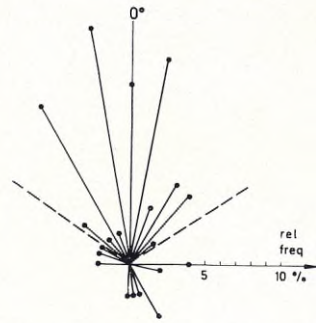


Fig. A 4. Polar diagram of the frequency distribution of observed turns sum of experiments C80 and D80.

tion between successive intervals were computed. The frequency of turns of different magnitude is shown in Fig. A 4. The 100 m uncertainty of the positions, and the short mean displacement, approximately 500 m during an active interval, leads to considerable uncertainty in determining the turning angle. An error of up to 50 deg is possible on this ground.

Statistical analysis

The movements of an "undisturbed" salmon are neither straight nor steady. Any disturbance due to the electromagnet therefore must be detected superimposed on a background level of spontaneous changes in swimming speed and direction.

To facilitate this the data was analysed in the following way:

- For a point in time separating two observation intervals two different behaviours were defined.
- I A change of activity, defined as a change in ground speed from less than 22.5 cm/s to higher or *vice versa*.
- II A significant turn, defined as a change in active swimming direction, compared to the direction during the preceding active interval, larger than 50 deg.

The total of observations of occurrences and non-occurrences of one behaviour can be regarded as a finite population with a known frequency of

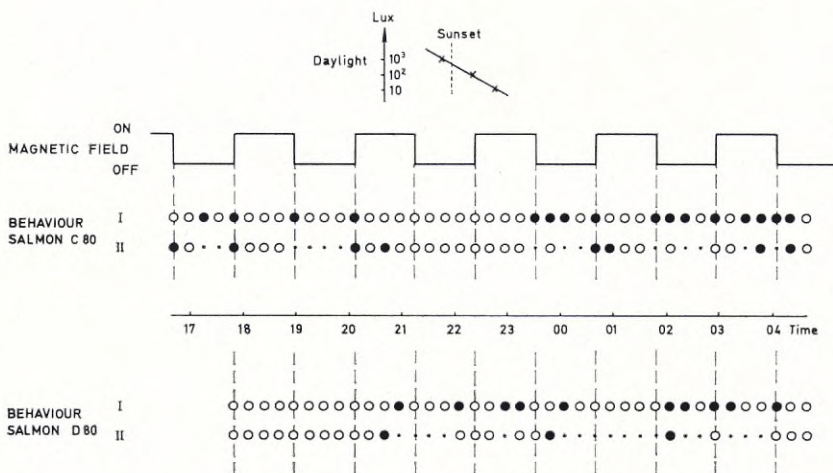


Fig. A 5. Time diagram, showing the occurrences of changes from swimming to non-swimming and large turns (behaviour I and II respectively). Filled circle; behaviour observed, open circle; behaviour not observed, dot; event not defined.

the behaviour. We wished to test the null hypothesis that the behaviour is independent of the switching on and off of the magnetic field. If this hypothesis is true, the observations which are simultaneous with changes of the magnetic field constitute a random sample, taken without replacement from this population. In this case the hypergeometric probability distribution is appropriate. The observed number of occurrences of behaviour I in the sample from experiment C 80 is 8, and the probability of finding 8 or more events in a sample of 11 is 0.0061. Behaviour II was observed 4 times in a sample of 7, and the probability of finding 4 or more events in this case becomes 0.068. If we look at the corresponding sample, taken at the same time 24 hours later in experiment D 80, we can calculate the probabilities 0.5 and 0.3 for the observed number of events of type I and II respectively.

If we exclude those points in time when there was a change of the field the relative frequencies of behaviours I and II become 24 % and 17 % respectively, for experiment C 80. This compares well with that seen in D 80, where the corresponding frequencies are 25 % and 14 %.

Discussion

The calculations above show that in the experiment with the coil there is a correlation between the changes of activity and the changes of the magnetic field, which is significant at the 1 % level. The correlation with observable turns is less pronounced, but still significant at the 10 % level.

In addition to these measurements on the recorded trajectory, more subjective observations were made during the tracking. In several instances the change from motionless drift to swimming could be heard as a slight Doppler-shift of the

transmitter frequency, and these changes occurred just when the electromagnet switched on. The timing of some of the turns could also be determined to coincide closely with changes of the magnetic field.

The conclusion that can be drawn from this experiment is that the salmon was able to sense the state of the electro-magnet. The physiological mechanism for this could be direct magnetoreception, but electroreception can not be ruled out. If the fish is moving the magnetic field will induce an electric field in the water close to the coil, which is of the same order of magnitude as those which ROMMEL and McCLEAVE (1973) have shown that a salmon can sense. The changing field when the magnet is switched on or off will also induce a transient current field in the water, which could be detected by the fish even if it is motionless.

Detection by other means seems improbable. All electric leads were well insulated, and there were no acoustic or mechanic changes associated with the switching.

There is no clear interpretation of this experiment with regard to the way geomagnetic or geoelectric fields are used by the salmon as navigation aids. It seems probable that these orientation mechanisms would be of chief value during the long distance, open water phase of the migration. During the estuarine part olfactory cues probably dominate the orientation. The fish which were used for this experiment were caught in the archipelago and must have been orientating for some time in such a hypothetical estuarine mode. They were moved into relatively open water to trigger the long-distance migratory behaviour, but the translocation may well have disturbed the salmon so much that what is seen in the short period of tracking has little resemblance to the normal behaviour.

Ultrasonic Tracking of Atlantic Salmon (*Salmo salar* L.) – II. Swimming Depth and Temperature Stratification

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ABSTRACT

The swimming depth of 8 adult salmon was monitored continuously during tracking in the coastal zone at the time of spawning migration. A new depth-sensitive transmitter was used and is described. A technique for continuous recording and automatic decoding of the swimming depth data is presented.

A behaviour common to all individuals were occasional rapid excursions down to the main thermocline, or, if the initial swimming depth was in the stratification, upwards to the mixed layer. The amplitude of the dives was 5 to 15 m, and seemed related to the distance to the thermocline. The vertical velocities of the dives was of the order of magnitude 0.1 m/s.

The detailed vertical temperature distribution along the trajectory was recorded. A comparison of the temperature field and the swimming depth indicated that the salmon tended to follow finestructure gradient layers in the quasi-mixed surface layer or in the thermocline.

These observations are interpreted using a model for olfactive orientation, where the salmon uses information found in the vertical to choose horizontal direction. The dives are seen as exploratory searches of the vertical distribution of a home stream odour. By choosing the finestructure gradient layer with the maximum concentration difference and then orientating against the direction of the local shear, the salmon has a strategy which would lead towards the origin of the olfactant.

Measurements which indicate a slightly elevated body temperature in salmon, and some faculty of thermoregulation, are discussed.

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I. INTRODUCTION

A number of ultrasonic tracking experiments on migrating adult salmon were described in an accompanying article ("Ultrasonic tracking of Atlantic salmon (*Salmo salar*) — I. Movements in coastal regions" subsequently referred to as A). Initially trackings were undertaken in the estuary of the Lule river, and in some of these pressure-sensitive transmitters were used to measure the swimming depth of the salmon. To further investi-

gate the vertical movements in relation to the hydrography a series of experiments was done in Lake Vänern. A lake was chosen because in freshwater the stratification can be entirely determined by the measurement of temperature alone. The vertical temperature stratification was recorded along the tracks, and the swimming depth was monitored continuously. This article will present the observations and discuss a possible interpretation of them.

The concept of vertical temperature finestructure is central to this investigation and an elementary account of the properties of the finestructure features in the thermocline is given in section III.

The experiment shows that the salmon tended to move at isothermal surfaces rather than at fixed depths and that the movements took place preferentially along thin layers with strong vertical gradients. A characteristic behaviour was an occasional vertical excursion through most of the thermocline.

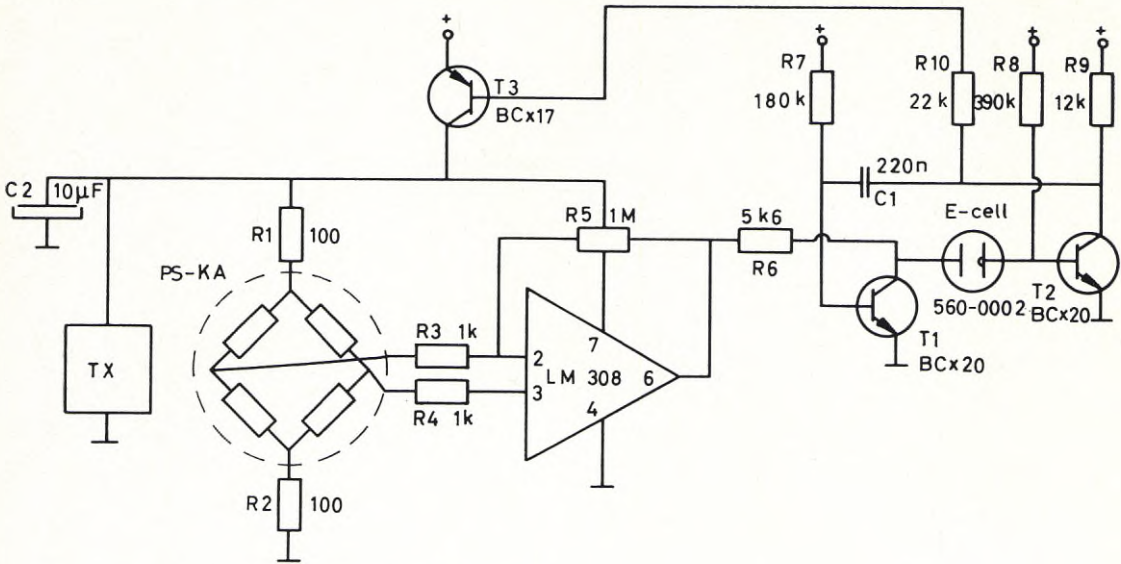


Fig. 1. Circuit diagram of the pressure-sensitive transmitter.

This is the first time that fish behaviour has been studied in relation to the details of the stratification, and the observations suggest that the small-scale structures of the temperature distribution are indeed detected and probably utilized by the salmon. A hypothesis is forwarded that the salmon uses information found in the vertical finestructure as cues for horizontal orientation.

II. MATERIAL AND METHODS

The tracking procedure and the handling of the salmon used in the experiments are described in A.

The pressure transmitter

The pressure-sensitive transmitter used in these experiments was designed to give a high resolution of depth variations, a stable calibration and a linear relation between pressure and the signal pulse period. The best choice of pressure transducer with respect to temperature stability, linearity and hysteresis is a strain-gauge type. As this kind of transducer has a low resistance and a high current drain it was necessary to limit the power consumption by activating the transducer intermittently with a short-duty cycle. This was done using an

E-cell, a miniature coulometer which acts as a current integrator. The circuit diagram of the transmitter is shown in Fig. 1. During the duty cycle, determined by R7 and C1, the transistor T2 conducts and the transducer is activated via T3. The amplified output from the transducer is integrated in the E-cell. When T1 becomes conductive T3 is cut off and the transducer, amplifier and the transmitter oscillator (TX) are inactivated. During a time which is strictly proportional to the earlier output voltage of the transducer a current will flow through the E-cell via T1 and R8, and the sequence is then repeated.

The component values were chosen to give a 30 ms pulse length and a pulse repetition period varying from 0.5 to 1.5 s over the full pressure range. The strain gauge transducer (Kyowa Electronic Instruments) had a diameter of 6 mm and a thickness of approximately 1 mm. The E-cell is manufactured by Plessey Electro-Products. Size and other specifications of the transmitter are given in A, Table 1. Expressed as percentage change of the full scale range the linearity of the pressure signal was 0.025 %, the temperature coefficient was ± 0.15 %/deg and the drift due to battery voltage change was approximately 0.4 %/day. The hysteresis depended on the magni-

Table 1. *Data for the experiments with pressure-sensitive transmitter.*

Exp	Salmon		Tracking		Transmitter range (m)	Observed swimming depth range (m)		
	Weight (kg)	Sex	Length (km)	Time (h)		min	median	max
D 78	9.5	♂	0	12	20			
E	6		58.0	34.5	20	0	4	18
F	5		32.6	30.5	20	1	5	13
G	6		5.3	3.6	20	1	2	3
I	5	♀	28.6	16.5	20	4	7	11
A 79	7		0	60	20			
B	5		14.3	7.8	50	7	10	17
C	3		36.1	20.0	20	1	4	14
A 80	4		8.0	10.5	20	1	9	11
B	3.5		15.3	31.3	20	3	13	24
C	6	31.2	23.9	100	0	10	16	

tude of the pressure cycle which is experienced, and was ± 0.6 – 0.7 % of this. The time constants for a change in pressure or temperature were 10 and 60 s respectively.

The transmitters were calibrated in the sea immediately before tracking, so that the temperature conditions at calibration were similar to those during the experiment. In this way the temperature effects were proportional to the anomaly of the *in situ* temperatures during the tracking, rather than to the full temperature range. Calibration was determined by attaching the transmitter to the T–D sond used for the temperature measurements. A small hydrophone in the sond picked up the signal and the pulse period was measured with a timer-counter to within 1 ms. As the pressure transducer in the temperature sond was used in the calibration any absolute errors in the depth measurements are eliminated when the swimming depth is compared to the measurements of the temperature distribution.

Temperature measurements

To measure the vertical temperature profile a temperature-depth sond with a strain-gauge pressure transducer and a fast-response thermistor was used. To resolve fine details of the stratification avoiding disturbance from the movements of the boat the instrument was made essentially free-falling. The thermistor, together with the pressure

gauge and the hydrophone, was mounted in a protecting cage below a buoyant cone with the apex pointing downwards. A thin cable was paid out in excess during the descent of the instrument and was used for recovery when the profile was completed. The buoyancy and drag of the cone was adjusted to regulate the rate of descent to approximately 0.5 m/s.

The vertical resolution of the thermistor was of the order 10 cm with this velocity. The temperature measuring circuit is described in PETRÉN 1972 and the linearity and accuracy were better than 0.1 degree. Recording was done on a X–Y plotter. The analog recordings were digitized and used in this form for the data plotting.

Data processing

During tracking close to the city of Luleå in 1978 the swimming depth was monitored manually, by measuring the duration of 10 pulse periods with a stop-watch. With a 20 m transmitter, having typically a 50 ms/m calibration factor, this gave a ± 0.2 m uncertainty due to the timing error alone.

During 1979 and 1980 the signal was recorded on a Sony TCD5 cassette tape recorder. The tapes were analysed using the decoding system shown as a block diagram in Fig. 2. The amplified audio signal was fed to a comparator with an adjustable reference level. The audio pulse was

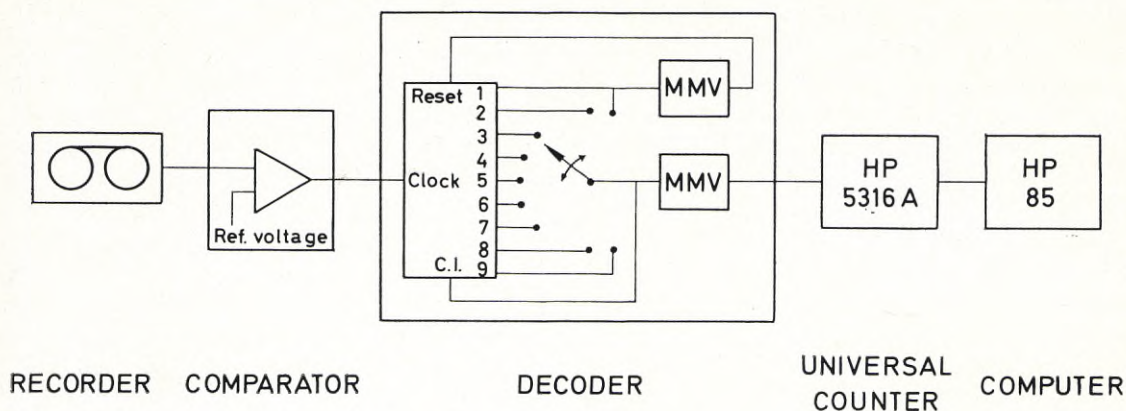


Fig. 2. Block diagram of the decoding system for swimming-depth data.

thereafter represented by a train of 10–15 pulses, depending on the tone frequency. This train of pulses clocked a decade counter. The first pulse which arrived triggered a monostable multivibrator (MMV), which after a predetermined time of 4–50 ms reset the counter. A selectable number of from 2 to 9 pulses had to arrive during this time to trigger the next MMV and inhibit the counter. This counter configuration acted as an ideal high pass filter, with the cut-off frequency determined by the number of pulses and the pre-set time interval. At the same time it was practically immune to spurious transients of any frequency. The time between subsequent pulses coming from the decoder was measured with a universal counter connected to a Hewlett-Packard 85 computer. The computer accumulated all the pulse period measurements from one cassette track and then processed them to eliminate all obvious errors. The pulse periods were converted to swimming depth and an average was made from all available pulses during consecutive 10 s intervals. The data was stored on a digital cassette.

The errors in the pulse period measurements were caused by wow and flutter of the tape recorder and by the uncertainty in discrimination of the leading edge of the audio pulses. The former was approximately 1 ‰, which corresponds to 2 cm for a 20 m transmitter. The latter error could be as large as 10 ms, or 20 cm, for a single pulse period, when the signal strength varied considerably. In the averaging procedure this contribution is cancelled and is reduced by

the number of pulses present. An additional uncertainty in the conversion to swimming depth was introduced by the Doppler shift of the ultrasonic pulses when the tracking boat and the fish moved relative to each other. A 1.5 m/s relative velocity gives an error of approximately 1 ms, or again 2 cm. These errors combined to give a typical noise level of the decoded and averaged swimming depth which was ± 5 cm for the 20 m range transmitter.

Neurotomy of anosmic salmon

The salmon (B 80) deprived of the sense of smell was anaesthetized in approximately 100 ppm MS 222 until no response was registered on pinching the anal fin. Incisions were made anterior to the nostrils, cutting the olfactory nerves. The incisions were closed with Histacryl (Braun GmbH). As an additional precaution the entrances to the nasal pits were sealed with Histacryl to prevent water flow through the olfactory organ.

The ultrasonic tag was inserted and the fish allowed to recover for 12 hours before release.

III. FINESTRUCTURE IN THE THERMOCLINE

The introduction of modern sounding instruments in oceanography has led to the discovery of ever finer scales in the vertical distribution of hydrographic parameters. Based on what can be resolved with a standard conductivity-tempera-

ture-depth recorder (CTD) and what must be studied with free-falling instruments the terms finestructure (vertical scale 100—1 m) and microstructure (less than 1 m vertical scale) are used. In this section I will give an elementary account of vertical finestructure (including scales down to 0.1 m in the term) as found in the near-shore regions in strongly stratified waters. Comprehensive and recent reviews of the subject in general can be found in MUNK 1981, GREGG and BRISCOE 1979 and in the monograph by FEDEROV 1978.

A temperature profile made with a high vertical resolution will always show irregular, often step-like structures. Almost homogeneous layers alternate with layers where the temperature changes rapidly. The thickness of both kinds of layers varies from a few metres to less than 0.1 m. The vertical distributions of all other hydrographic parameters, such as current, salinity or concentration of chemical substances, parallels that of the temperature. Although the sign and magnitude of the gradients of the other parameters can be quite different the rapid changes occur at the same depths as that of the temperature.

Characteristic of many of these structures is a strong anisotropy, the horizontal scales are much larger than the vertical. Typically a homogeneous layer of 1 m thickness can be traced for 100 to 1,000 m horizontally. Other structures are the result of the straining of the stratification by internal waves, and for these the coherence is less in the horizontal.

The vertical rate of change of temperature in a layer with a strong gradient can be up to two orders of magnitude larger than the mean gradient in the thermocline (10 deg/m). Dye injected into a gradient layer will spread out horizontally to a thin sheet of kilometre dimensions and can be followed for several hours, which shows both the essentially laminar conditions in the layer and the concentration of the current shear to the temperature gradient layer (KULLENBERG *et al.* 1973).

The processes that generate the finestructure are not fully unravelled, and several generation mechanisms can be present at the same time. In coastal waters the generation of locally well-mixed water masses and the subsequent interleaving of these seems to be an important process.

Temperature fluctuations caused by heating and cooling at the surface, combined with evaporation and precipitation which change the salinity, will cause slightly different densities in different bays and sounds upon wind mixing. When the wind decreases, gravity will spread the water masses at their approximate density levels in the upper thermocline or at the surface. This mode of finestructure production is discussed for the oceanic case in STOMMEL and FEDEROV 1966. Typically the lifetime of the interleaving layers will be several days and the horizontal extent large.

Cross-frontal mixing and overturning of internal waves will also create well-mixed water volumes which spread at their density levels. The volumes involved are less than in the interleaving case, and the horizontal extent of these intrusions will become smaller. The ratio of the horizontal to the vertical scale will, however, become of the order 100 to 1,000 before the structure disappears.

IV. RESULTS

In all 11 salmon were tracked using depth sensitive transmitters. Some general data about these salmon and experiments are collected in Table 1. Details about the horizontal movements and activity patterns as well as charts with the trajectories are found in A. Survey maps showing the location of places mentioned in the description of the experiments are also found in A.

In two of the experiments the salmon remained immobile at the bottom after release (D 78 and A 79), and in one (G 78) the duration of the tracking was too short to furnish adequate data. The other experiments will be presented below in the form of a time/depth diagram of the swimming depth and the gross thermal structure. As an aid to comparison of the experiments all diagrams are drawn with either one of two constant ratios of time- and depth scale. When the salmon is moving the diagrams can be interpreted as vertical sections along the trajectory. Assuming a mean swimming speed of 0.5 m/s the ratios which were used correspond to horizontal scales that are contracted 800 and 2,500 times the depth scale.

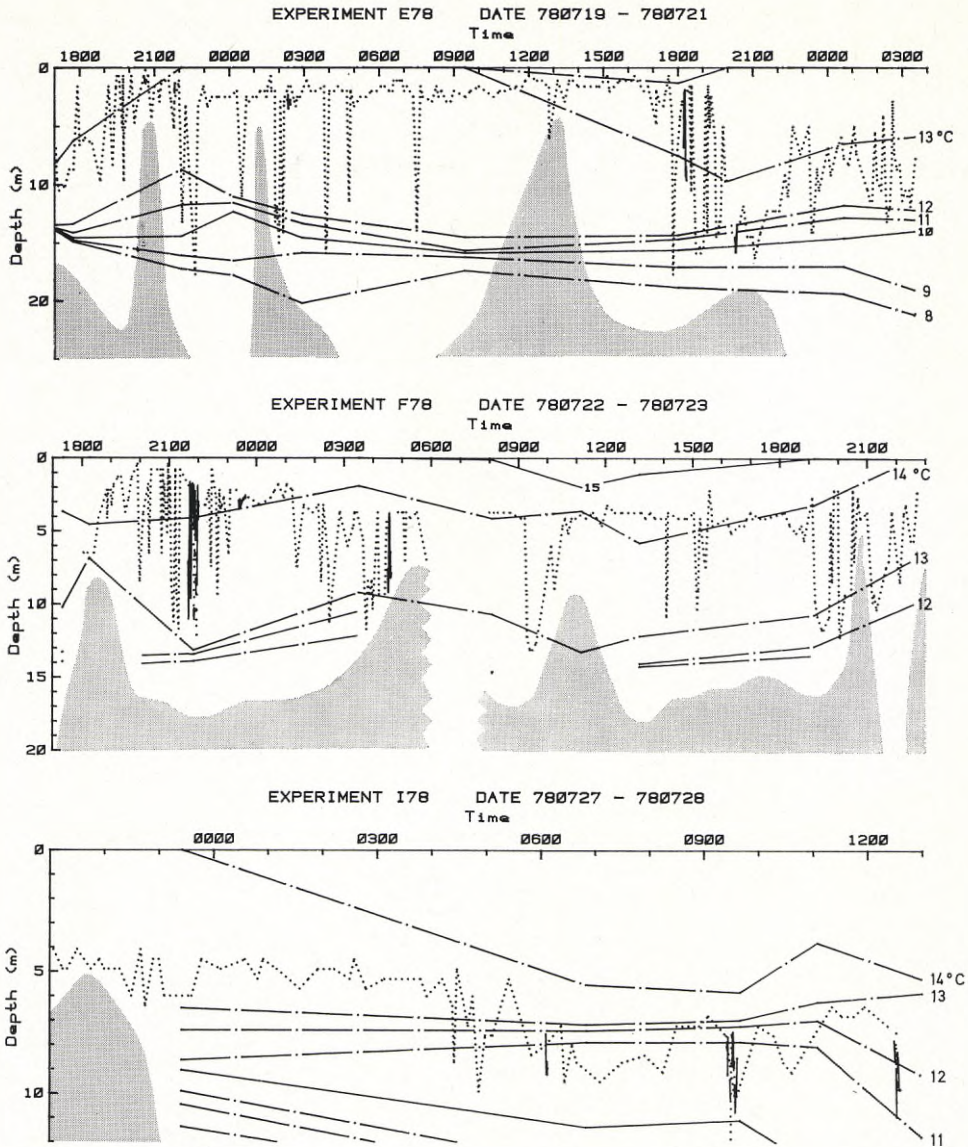


Fig. 3 a—c. Time series of the swimming-depth and the gross temperature stratification for trackings in Luleå 1978. The dotted line connects discrete points of manually recorded data. The shading shows the approximate bottom contour along the trajectory. The equivalent length to depth ratio is 2,500 with a swimming speed of 50 cm/s.

Comments to individual tracks

E78 — this salmon was released in the outer archipelago off the city of Luleå and was recaptured 6 days later in the estuary of the Pite river, south of Luleå. The time/depth diagram is shown in Fig. 3 a. In this experiment, as in all during 1978, the pulse period measurements were made manually. The brief deep dives that are seen

could be heard very clearly when they occurred and the maximum depth was checked as accurately as possible. Some dives might, however, have been undetected during periods when the noise from the moving boat masked the signal.

At 21⁰⁰ the salmon passed a sill and moved out on an open stretch of water, where she moved WSW for 20 hours, from the Lule archipelago to

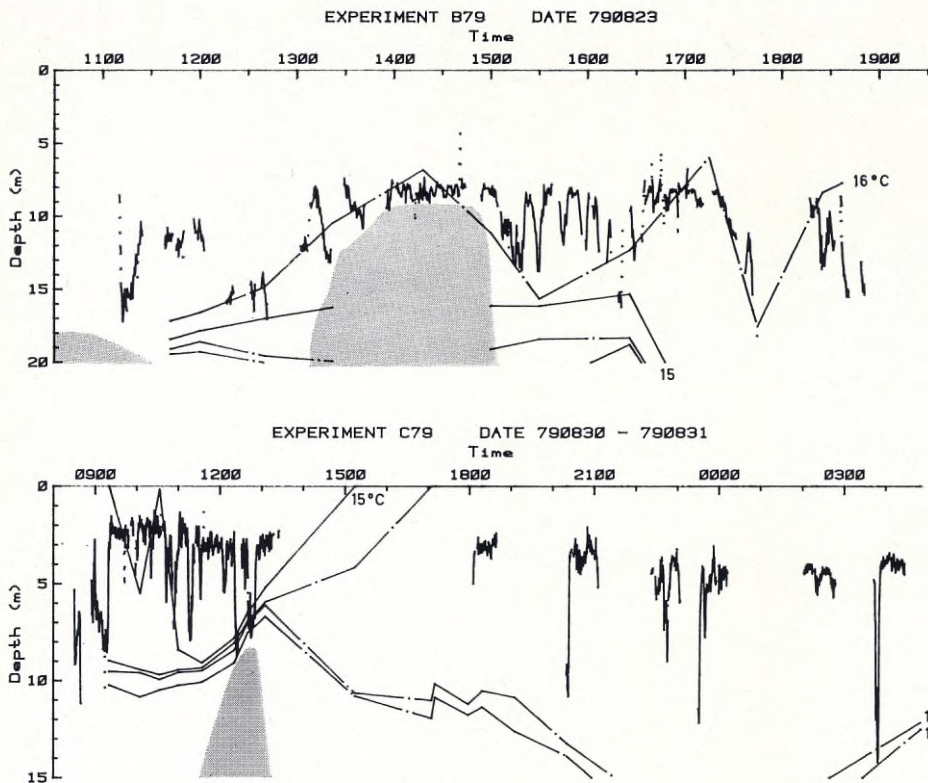


Fig. 4 a—b. Swimming depths recorded during tracking in Lake Vänern 1979. The swimming depth is averaged in 10 s intervals. The equivalent length to depth ratio is 800 for a) and 2,500 for b). The spacing of the isotherms is 1 deg.

the outskirts of the Pite archipelago. The open water distance was approximately 30 km. The salmon passed two shallow banks during this time, at 01⁰⁰ and 13⁰⁰ on the second day. At these times the dives may have reached the bottom, but otherwise the dives were down to the level of the main thermocline. From 18⁰⁰ on the second day to 04⁰⁰ on the third, when tracking was abandoned, the salmon milled around between the outer islands. An expanded plot of a short period of continuous recording of the swimming depth is given in Fig. 6. The turning points of the dive coincide with the layers of strong gradient at 2 and 9 m depth.

F 78 — this salmon was recaptured 9 days after release in the estuary of the Kalix river north of Luleå, indicating that she was a strayer in the Lule river estuary.

Immediately after release the salmon moved

into a bay between Sandö and Junkö. During the following 26 hours it moved in a complicated path over most of the bay, alternating between passive periods of mid-water drift and milling or erratic movements. At 21⁰⁰ on the second day it passed through a sound to the Germandöfjärd, turned south and headed out to sea when the tracking was terminated.

As in the case of E 78 numerous short dives were observed and measured. Periods with continuous recording of the swimming depth are included in Fig. 3 b at 21⁴⁰, 23²⁰ and 04³⁰ of the second day, but details cannot be seen at this scale. An expanded plot of one of these continuous swimming depth records is shown in Fig. 7. This recording shows a succession of dives, with turning points at the temperature inversion layer at 2 m and at some finescale steps at 11—12 m.

I 78 — During that part of the track shown in

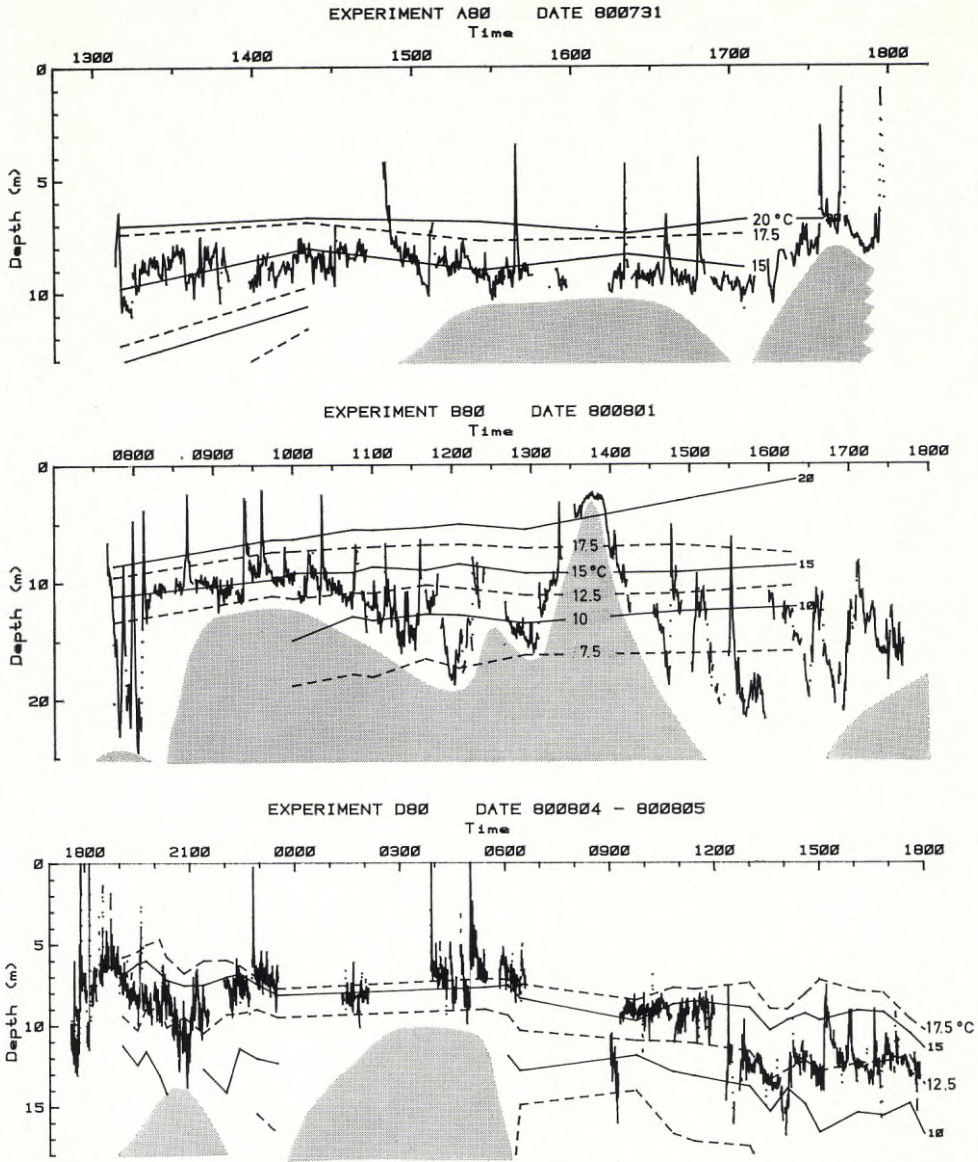


Fig. 5 a—c. Swimming depths recorded during trackings in Lake Vänern 1980. The equivalent length to depth ratio is 800 for a) and b) and 2,500 for c). The spacing of the isotherms is 2.5 deg.

Fig. 3 c the salmon moved steadily on a SE course, from the Brändöfjärd out to open sea. This salmon moved in the main thermocline, making dives both up- and downwards from the mean swimming level. The dives were not clearly audible during the tracking as in F and E 78, so the manual measurements give a smoothed depth curve. Short recordings at 06⁰⁰, 09⁰⁰ and 12⁰⁰ show

dives with the same vertical velocities as were observed in the other experiments, and amplitudes up to 5 m.

B 79 — During tracking in Lake Vänern 1979, the autumn cooling of the surface layer had begun. In the Säterholmsfjärd, where the trackings were started, the surface layer contained several gradient layers with approximately 0.1 deg temperature

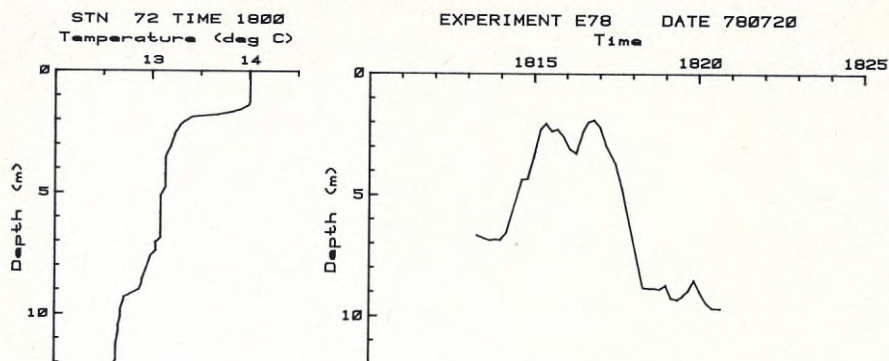


Fig. 6. Expanded portion of swimming depth record, compared to simultaneous temperature profile. Swimming depths are successive 10 s averages.

differences. Frequently the swimming depths observed at the time of a temperature recording could be associated with some of these gradient layers. The time and distance between the temperature drops were, however, generally too large to trace the thermal finestructure horizontally.

Fig. 4 a shows the swimming depth recordings of B 79. After release the salmon crossed the Säterholmsfjärden and arrived at 13³⁰ in a shallow area with several salmon nets. It stayed among the nets making intermittent movements until 15⁰⁰, when it crossed over the sound at Söökojan turned back and then moved south out of the sound towards Värmlandssjön. Around 17¹⁵ it cut obliquely across a front that was visible at the surface. Fig. 8 shows an expanded plot of this part of the tracking.

C 79 — This salmon crossed the Säterholmsfjärd and passed through the sound at Söökojan at 12⁰⁰—13⁰⁰. In the Värmlandssjön it headed nearly due south for 17 hours, moving at the highest speeds seen in any of the trackings (1.3 m/s).

Swimming depths are shown in Fig. 4 b. The observations in relation to temperature structure were similar to those of B 79 in the Säterholmsfjärd. In the Värmlandssjön the salmon moved at depths where the temperature was constant to within less than 0.05 deg. Dives down to the thermocline were seen. There were large gaps in the recordings and the tracking had to be terminated due to a technical fault.

A 80 — The trackings in 1980 were made earlier in the year than those in 1979. The tempera-

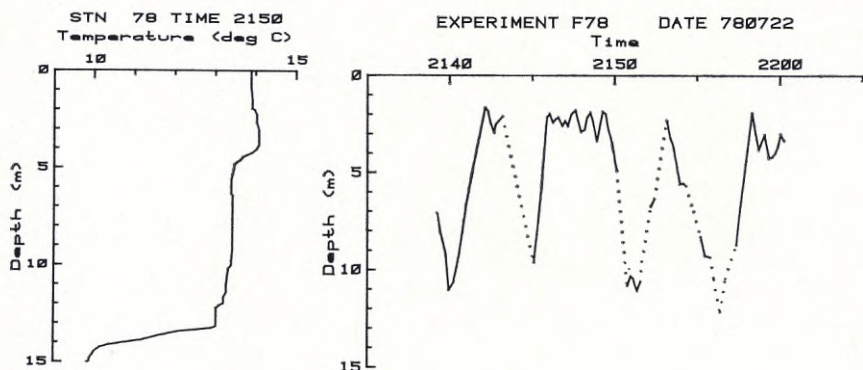


Fig. 7. Example of rapid succession of deep dives. Intervals where data are missing for periods of from 20 to 60 s are interpolated with a dotted line.

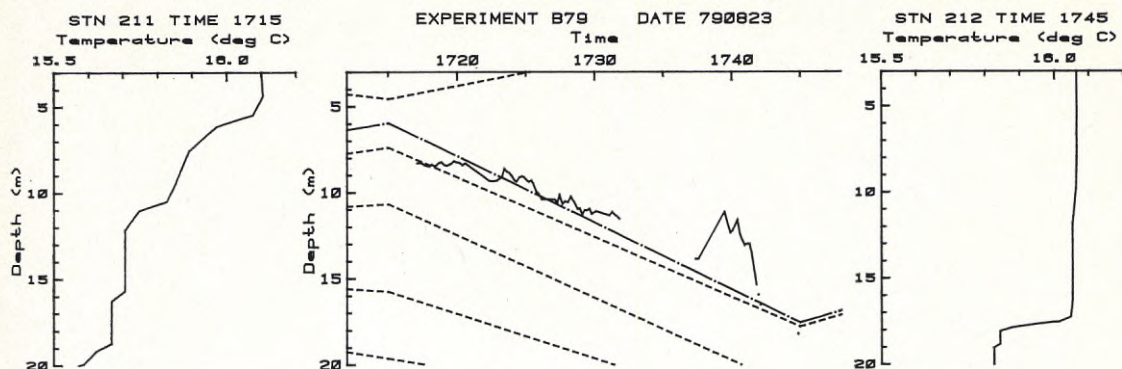


Fig. 8. Swimming depth during passage of a thermal front. The isotherms are drawn with a spacing of 0.1 deg.

ture of the surface layer was higher and the stratification stronger. The salmon A 80 was handled at the 20°C surface water temperature during tagging, the other fish were kept and handled in water with a temperature of less than 15°C, as described in A. The stress during handling may be the reason for the salmon staying on the bottom at 23 m depth for 5 hours after release. From 13⁰⁰ the salmon moved within the Säterholmsfjärd. As is seen in Fig. 5 a the swimming depth was below a sharp temperature gradient, in stratified water and with dives directed upwards, into the surface layer. During the first 2 hours the movements were in 20—15 m deep water. From this period an expanded plot is shown in Fig. 9. The salmon moved in a quasi-homogeneous layer with a temperature 14.5—15.5°C, turning at the layers of strong temperature gradient above and below.

At 15⁰⁰ the salmon entered a narrow channel between an island and a shallow bank. From then on the salmon was in contact with the bottom most of the time, making short dives up through the thermocline. Contact was lost due to the difficult tracking conditions with a strong refraction of the sound in the sharp thermal gradients.

B 80 — This salmon was made anosmic by neurotomy. During the first 10 hours of tracking the horizontal movements (A Fig. 6 b) did not obviously deviate from that seen in untreated salmon. The salmon moved out into the Värmlandssjön, veered west and moved at speeds comparable to those seen in other trackings along the arch of islands. Around 20⁰⁰ the salmon reached a small bay and stayed there with few and short movements for the next 20 hours.

As seen in the vertical, however, the behaviour was quite different from that seen in the other

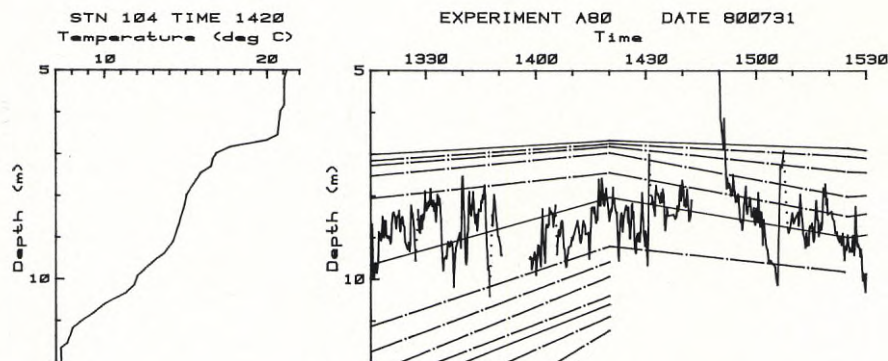


Fig. 9. Expanded portion of the record in Fig. 5 a showing movements along a quasi-homogeneous layer. Spacing of the isotherms; 1 deg.

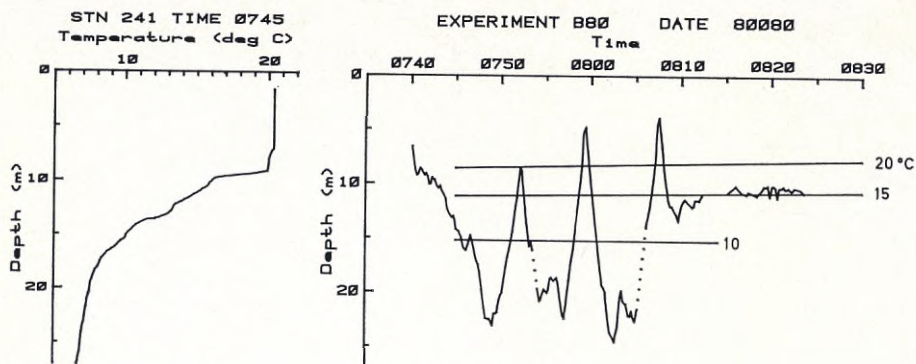


Fig. 10. The dives made immediately upon release of anosmic salmon.

salmon. Fig. 5 b shows the first 10 hours, and it can be seen that the movement was along the bottom for most of the time. There were numerous dives up through the thermocline. There was no specific depth or temperature level at which the salmon tended to stay. Immediately after release there was a series of dramatic dives up and down

through most of the water column. This part of the track is shown expanded in Fig. 10.

D 80 — In this experiment the salmon was relocated and released in open water in the Värmlandssjön (the reason is explained in the Appendix of A).

During the first part of the tracking the salmon

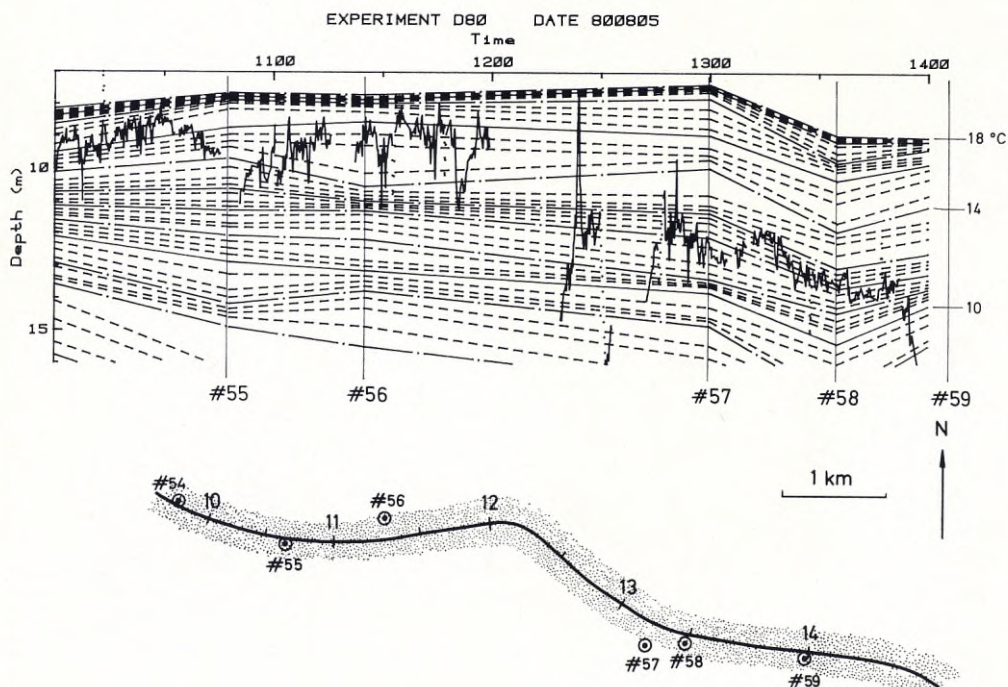


Fig. 11. Part of the swimming depth record of salmon D80. The thermal field is drawn with 0.25 deg spacing. The trajectory of the salmon during the same time period is shown with 30 min time marks and the uncertainty of the positioning indicated by the shading.

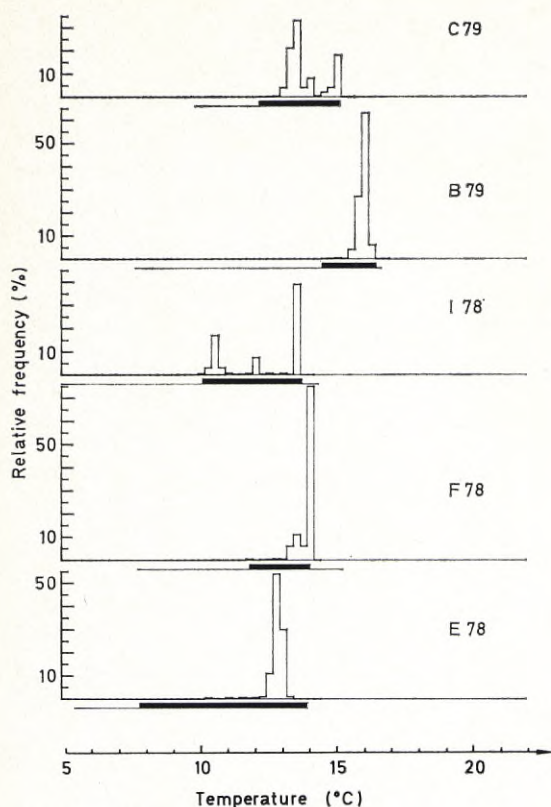


Fig. 12. Relative frequency of time spent at different 0.25 deg temperature intervals. The heavy line shows the extreme temperature range in which the salmon was observed, the thin line shows the temperature range which was available along the track.

moved irregularly and was passive in mid-water for several periods. From 06⁰⁰ on the second day it started a continuous movement which was steadily towards east. The depth-time diagram is shown in Fig. 5 c.

The temperature profiling was undertaken from a second boat in this experiment. In this way the temperature measurements could be done without interference to the tracking and the spacing of the profiles was reasonably close even when the salmon was moving continuously. Fig. 11 shows an expanded plot of a portion of the track. In this example some of the finestructure layers in the thermocline can be traced between several profiles. As for example a layer with strong vertical gradient at 12–13°C. From 10⁰⁰ to 12⁰⁰

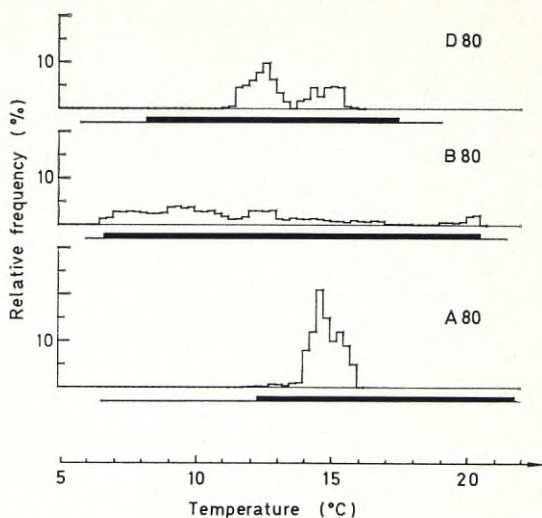


Fig. 13. Same as Fig. 12. The frequency scale is increased by a factor of 2.

the swimming depth was at the level of a gradient layer between 14.5 and 15°C. From 12⁰⁰ to 12¹⁵ there was a succession of two or three dives down and up through the main part of the thermocline. The strong stratification caused a sudden shift in the signal strength when the salmon dived and the first dive is not recorded. From 12²⁰ the salmon changed swimming depth and seemed to follow the 12–13°C gradient layer.

Temperature selection

Using time — depth diagrams of the swimming depth and the temperature stratification the total residence time in different temperature intervals has been measured. Fig. 12 shows the relative frequency of time spent in 0.25 deg intervals for the whole duration of the trackings of 1978 and 1979. During 1980 the salmon moved in a stronger stratification. Because of this the result of the calculation is more sensitive to errors in interpolation of the isotherms between stations. For these experiments the frequency distribution has been calculated for periods of the tracking where the salmon was active and at the same time the coverage of swimming depth and temperature was reasonably complete. The following periods were used:

Exp	Time interval	Date
A 80	13 ¹⁰ —16 ⁰⁰	July 31, 1980
B 80	10 ⁰⁰ —16 ⁰⁰	August 1, 1980
D 80	10 ⁰⁰ —18 ⁰⁰	August 5, 1980

The result is shown in Fig. 13. The total range of temperatures that were available to the salmon, and the extreme range which the salmon encountered at any time are also indicated in Figs. 12—13.

It is seen that the salmon spend a large proportion of time in a temperature interval which is narrow compared to the available range. In some experiments, I 78, C 79 and D 80, the distribution is multimodal. The anosmic salmon, B 80, shows a strongly deviating distribution, which is almost flat and extends over the whole available temperature range.

The median temperatures selected were:

Exp	°C
E 78	13.0
F	14.1
I	13.0
B 79	16.0
C	13.6
A 80	14.8
B	10.5
D	12.9

Brief dives

A behaviour which is conspicuous and displayed by all the salmon was the occasional brief dive. Characteristically the amplitude of the excursion was 5—10 m, and the salmon normally returned to the previous swimming depth within 3 to 10 minutes. An analysis of the vertical velocities shows that they rarely exceeded 0.2 m/s. Commonly the rate of descent was 0.1 m/s and the ascent slightly faster; 15—0.2 m/s. This means that with the observed horizontal velocities, which were in the range 0.4—0.5 m/s, the salmon dived with an inclination of approximately 10 deg to the horizontal plane and could swim at an angle of up to 25 deg during the upward phase. The frequency of the dives was of the order of one per hour.

V. DISCUSSION

Relation to the temperature field

The temperature preferences of salmon have been studied in laboratory experiments, for example a final preferendum of approximately 17°C was found for juvenile Atlantic salmon (JAVAID and ANDERSON 1967).

In the present experiments there was no indication that the absolute value of the temperature was primarily responsible for the salmon's choice of temperature level. During periods with the same available temperature range different salmon choose different temperatures, and one individual could alternate between two or more levels of temperature as seen in I 78 and D 80.

The results in 1980 can be interpreted as a preference for temperatures less than the 19—22°C temperature in the surface layer. An alternative explanation is that during this period with intense heating of the surface layer the temperature of the river water was somewhat less than the surface lake water, and that the plume of river water intruded in the top of the thermocline, rather than spread at the surface.

Even if the preference of an absolute temperature is unclear there are numerous observations which show a relation between the swimming depth of the salmon and the vertical temperature stratification. Figs. 6 and 7 show examples where the turning points of dives and the levels of short periods of horizontal swimming coincided with gradient layers. This type of correlation of swimming depth and some finestructure feature at a single point in time is seen in a large number of cases. The considerable interval in time and space between the temperature profiles makes it difficult to identify individual gradient layers from one profile to the next. In some cases, as in Figs. 9, 8 and 11, this is possible to some degree, and there is a strong indication that the salmon follows a particular finestructure layer for long periods.

Dives

The brief dives are seen in all the trackings. When the salmon moved in the weakly stratified upper layer the direction of the dives was downwards, but in cases when the movement was in the main

thermocline, as in A 80 and D 80, the direction was upwards or both ways.

Dives with the same characteristics are reported by WAATEVIK (1980) from a single tracking of salmon in a Norwegian fjord. He noted a marked increase in frequency of dives during times when the salmon changed swimming direction and at narrow passages in the fjord, where the horizontal movement of the salmon became erratic. A similar tendency of increased diving activity is seen during periods of intermittent or milling movements in the present trackings. The diving behaviour and the movements along finestructure gradients can be explained as an orientation mechanism, and an attempt is made in the following formulation of a hypothesis.

Olfactive orientation

The importance of olfaction for salmon orientation and homing is well established (HASLER 1966, HASLER and SCHOLTZ 1978, BERTMAR and TOFT 1969). The role of olfaction in orientation is, however, not clear. The concentration of a chemical substance is a scalar quantity, without directional properties. The orientation mechanism can be of two types: response to a gradient of the concentration or a response to some other directional clue which is released by an olfactory stimulus. The different possibilities are discussed by HARDEN JONES (1968). He concludes that the gentle gradients found in natural waters are too weak to be detected by simultaneous comparison of concentration at the nares. A temporal comparison and detection of the gradient is possible, but in that case the fish must be able to orient to some other cue so that it can maintain or alter its direction after the period needed to make the comparison. The most likely types of orientation is the latter, where olfaction is a sign stimulus for orientation to something else, probably water currents.

A fundamental difficulty in rheotropism as an orientation mechanism is that the fish has to be in visual or tactile contact with a fixed reference to be able to determine the current direction. I would like to propose a model for salmon olfactive orientation which avoids this problem and fits the observations of the behaviour in relation to the thermal finestructure.

The essential idea is that orientation is based on information found in the vertical distributions of the olfactant and the local current, rather than in the horizontal concentration distribution or the absolute current directions. In the succession of finestructure layers at a given place and time there will be one gradient layer which contains the largest vertical concentration difference of that olfactive substance which is used by the salmon to recognize the home stream. This gradient layer is found by the salmon by swimming up and down through the water column. Across this gradient layer there will be a current shear, the direction of which is determined by the relative motion of the layer containing a large concentration of the home stream substance with respect to the layer with lower concentration above or below. In an estuarine situation the relative motion of the layer with the higher concentration will on average be away from the source of the substance. In any particular case the direction given by the shear can deviate considerably from the true direction to the river mouth, but statistically a choice of swimming direction against the relative motion of the high concentration layer will be appropriate. By occasional excursions through the stratification the salmon can check that the layer which it is following is still the one with the largest concentration contrast, and if not, switch to the new one. A strategy like this will lead the salmon towards the river mouth along a path which may be complex and contain detours, but which in the main is in the right direction.

The temporal comparison of concentration differences during a dive lasting a few minutes seems feasible. The possibility of detection of the local current shear is more uncertain. Typically the velocity difference can be 0.01–0.1 m/s across a layer of 10–100 cm thickness. Visual detection would be possible at least for the stronger shears. Other possibilities are the detection of the acceleration which is felt on crossing the layer, or the direct detection of the velocity difference across the body when the salmon is within the layer.

There are variations on the hypothesis, with other criteria for choosing the layer. One is to choose the quasi-homogeneous layer with the

highest concentration of the home stream substance, and to move against the relative motion of this layer with respect to the surrounding water, switching to the one which locally has the maximum concentration when the earlier one ends. Another is to choose the gradient layer with the largest shear, moving opposite to the relative direction of the water having a higher concentration of the olfactant. The statistical properties of these strategies are less clear, and no attempt has been made to estimate and compare the theoretical effectiveness of the different choices.

One set of observations which contains all the components in the hypothesis is the time-series presented in Fig. 11. The salmon follows a gradient layer, makes a number of dives, switches to a new gradient layer and continues, but on a different course. Support for the interpretation of the behaviour as an orientation based on olfactory cues is offered by the experiment with an anosmic salmon.

Anosmic salmon

It can be realized that the behaviour of the anosmic salmon differed dramatically from that of untreated salmon. The movement was along the bottom, a behaviour which was never seen for any extended period in the other trackings. The swimming depth of the anosmic salmon was completely unrelated to the temperature field, as is clearly seen in the frequency distribution in Fig. 13.

The salmon made dives through the thermocline which were of the same appearance as those seen in the other experiments but the frequency of large amplitude dives was somewhat higher, approximately 3 dives per hour during the first 10 hours.

The series of dives immediately after release was striking (Fig. 10), and it is tempting to interpret these, and the increased frequency of dives later in the experiment, as unsuccessful attempts to make olfactory searches in the vertical.

Conclusions

The swimming depth measurements gave several indications that salmon detected the small-scale

gradient layers in the thermocline and the surface layer. There were also several cases where the movement seemed to be along a particular gradient layer rather than at a constant depth.

The occasional dive was a behaviour, manifested by all the salmon, and it seems probable that this was an exploratory search of the vertical distribution of some parameter, as the direction of the dives was towards the thermocline, and the amplitude determined by the distance to the main thermocline.

The hypothesis that these behaviours are components of an orientation strategy based on olfactory cues is supported by the observation of the anomalous behaviour of one anosmic salmon.

The observation that fish are able to sense, and possibly to extract information from, the finestructure scales of the vertical temperature distribution may be of general significance to studies of the relation between fish behaviour and hydrography. Apart from the olfactory orientation mechanism discussed above other properties of the finestructure may be used by the fish. There are signatures in the microstructure that propagate far downstream from islands and other topographic features in the ocean (HOGG *et al.* 1978) and it is tempting to speculate that these could be utilized to localize say an offshore bank.

VI. ACKNOWLEDGMENTS

Those same people and financiers who were mentioned in A have also contributed to this work. I would like to restate the importance of LENNART BJÖRK's work in the development and manufacturing of the transmitters. I am also grateful to KJELL DØVING, who took the initiative to perform the experiment with the anosmic salmon, carried out the operation and participated in the field work of 1980. MAUREEN MOIR has corrected my English which is gratefully acknowledged.

VII. REFERENCES

- BERTMAR, G. and R. TOFT. 1969. Sensory mechanisms of homing in salmonid fish. I. Introductory experiments on the olfactory sense in grilse of Baltic salmon (*Salmon salar*). *Behaviour* 35 (3-4): 235-241.

- BJÖRK, L. 1977. Equipment for telemetry investigations. *Inform. Inst. Freshw. Res. Drottningholm* (16). 26 p. (In Swedish with English summary.)
- BRETT, J. R. 1965. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). *J. Fish. Res. Board Can.* 22(6): 1491—1501.
- CAREY, F. G., J. M. TEAL, J. W. KANWISHER, K. D. LAWSON and J. S. BECKETT. 1971. Warm-bodied fish. *Amer. Zool.* 11: 137—145.
- FEDEROV, K. N. 1978. The thermohaline fine-structure of the ocean. Pergamon Press, N.Y.
- GREGG, M. C. and M. G. BRISCOE. 1979. Internal waves, finestructure, microstructure and mixing in the ocean. *Rev. Geophys. Space Phys.* 17(7): 1524—1548.
- HARDEN JONES, F. R. 1968. Fish migration. Edward Arnold Ltd, London. 325 p.
- HASLER, A. D. 1966. Underwater guideposts. University of Wisconsin Press, Madison. 155 p.
- HASLER, A. D. and A. T. SCHOLZ. 1978. Olfactory imprinting in coho salmon (*Oncorhynchus kisutch*). p. 356—369. In *Animal migration, navigation and homing*. Eds.: K. Schmidt-Kornig and W. T. Kelton. Springer-Verlag, Berlin.
- HOGG, N. G., E. J. KATZ and T. B. SANFORD. 1978. Eddies, islands and mixing. *J. Geophys. Res.* 83: 2921—2938.
- JAVAI, M. Y. and J. M. ANDERSON. 1967. Thermal acclimation and temperature selection in Atlantic salmon (*Salmo salar*) and rainbow trout (*S. gairdneri*). *J. Fish Res. Board Can.* 24(7): 1507—1513.
- KULLENBERG, G. C. R. MURTHY and H. WESTERBERG. 1973. An experimental study of diffusion characteristics in the thermocline and hypolimnion regions of Lake Ontario. *Int. Ass. Great Lakes Res.*, Ann Arbor, Mich. *Proc. 16th Conf. Great Lakes Res.*: 774—790.
- MUNK, W. 1981. Internal waves and small-scale processes. p. 264—291. In *Evolution of physical oceanography*. Eds.: B. A. Warren and C. Wunsch. MIT Press, Cambridge, Mass.
- PETRÉN, O. 1972. A recording instrument measuring conductivity and temperature versus depth for use in shallow water. Univ. Gothenburg, *Rep. Inst. Oceanogr.* 5. 19 p.
- STOMMEL, H. and K. N. FEDEROV. 1966. Small-scale structure in temperature and salinity near Timor and Mindanao. *Tellus* 19: 306—325.
- WAATEVIK, E. 1980. Vandringstudier av laks (*Salmo salar* L.) i Sandsfjorden i Fyfylke ved hjelp av akustiske merker. Unpubl. thesis. Univ. Bergen. 76 p. (Mimeographed in Norwegian.)
- WOOD, C. M. and G. SHELTON. 1980. Cardiovascular dynamics and adrenergic responses of the rainbow trout *in vivo*. *J. Exp. Biol.* 87: 247—270.

APPENDIX:

A Note on Body Temperature

In 1976 attempts were made to study the temperature preferences and indirectly the swimming depth of the salmon with the help of temperature-telemetering tags placed in the stomach. It soon became apparent that the temperatures which were telemetered were higher than the recorded water temperature at any depth. The conclusion made at the time was that some error had been made in the calibration of the tag, and data was collected very sparingly.

Some time later one of the temperature tags was returned after recapture. This tag was fitted with a new battery and calibrated again. The new calibration deviated from the old one by only 0.1 deg maximum, significantly less than the 0.5—1 deg differences seen during the trackings in Luleå. In view of this, and the fact that elevated body temperatures are observed in tuna and some other fish (CAREY *et al.* 1971), one salmon was fitted with a temperature transmitter in the stomach, together with a depth-transmitter placed externally, during the trackings in 1979.

This experiment confirmed the results from 1976, showing a stomach temperature approximately 0.5 deg above that of the surrounding water. On one occasion the salmon moved below the thermocline, and an analysis of the changes of the stomach temperature during this time indicate that salmon may have some mechanism for active thermoregulation of the viscera.

Material and Methods

The temperature sensitive transmitter is described in Björk 1977. It was calibrated in the laboratory prior to the experiment and was accurate to 0.1 deg. The time constant of the transmitter was approximately 30 sec.

The carrier frequencies of the two transmitters used in 1979 were separated by 15 kHz. The hydrophone signal was fed to two receivers in parallel, each tuned to one of the transmitters. The audio signals were recorded on separate channels of the tape recorder and the pulse periods on the recordings were measured and processed as described in section II.

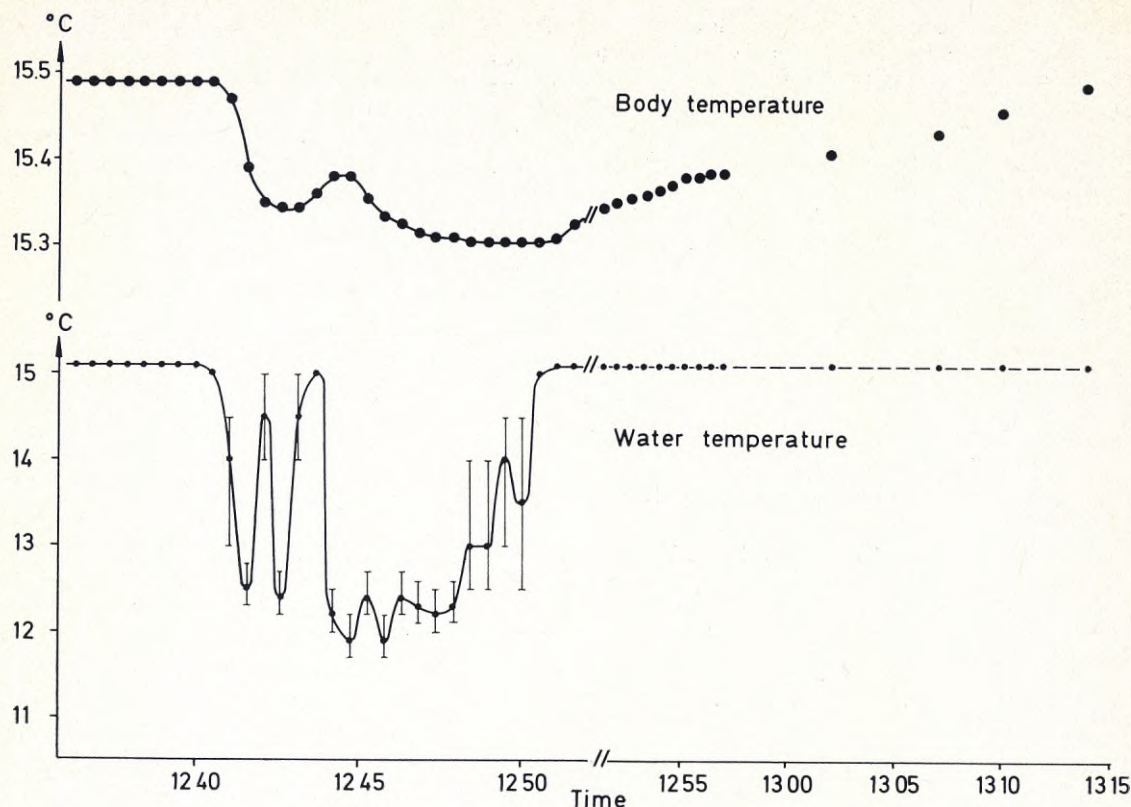


Fig. A 1. The variation of the body temperature, measured in the stomach, during an episode where the salmon moved below the thermocline. The water temperature is inferred from the observed swimming depth and the stratification, the bars indicate the uncertainty of the estimates. All points show a 60 s time average of the temperature.

The sensitivity of the temperature tag to a change in temperature was high compared to the absolute accuracy. The RMS noise level of the signal after decoding and averaging in 10 s time intervals was $1-2 \cdot 10^{-2}$ deg. Changes which occurred on a timescale of minutes were resolved to better than 10 mdeg.

The temperature of the ambient water was estimated from the measured temperature stratification and the swimming depth. Between the temperature stations a linear interpolation was made for the depth of the isotherms.

Results

In 1976 the observed temperature excess was

Exp	max	min
K 76	1.5	0.4
L 76	0.7	0.4

Since the difference involves the maximum water temperature the values represent lower limits to the true excess temperature. In experiment C 79 the minimum value of the excess was 0.4 deg and for the periods when the salmon stayed continuously in the surface water they ranged up to 0.7 deg.

In Fig. A 1 the temperature measurements are shown for a period when the salmon dived below the thermocline and stayed there for almost 10 minutes. The water temperature data are interpolated between profiles made at the times 12²⁰, 12⁴⁰ and 13⁰⁵. As the swimming depth was in the vicinity of a strong thermocline small deviations from linearity can give a large error in the estimate of water temperatures. The uncertainty is estimated to be 1–1.5 deg in the range 12.5–14.5°C, and approximately 0.5 deg

for the temperatures 12.5. In the surface layer the uncertainty is 0.05 deg.

Discussion

The expected body temperature of a fish should be very close to that of the ambient water temperature in the absence of a heat-exchange system. This is because the heating process, metabolism, is locked to the cooling that occurs when the blood passes through the gills; therefore the fish is unable to accumulate heat to raise its body-temperature (CAREY *et al.* 1971).

A simple model of the thermal balance of a fish can be used to analyse the data in Fig. A 1. The model fish is shown in Fig. A 2. The main assumption is that all heat exchange is through the gills. In that case the change in total heat content of the fish is the sum of the heat flux through the gills and the internal production of heat by metabolism.

$$\frac{dH}{dt} = qC(T_{IN} - T_{OUT}) + Q$$

C is the heat capacity of tissue and blood, H is the heat content and all other symbols are defined in the figure. As

$$H = MT_B C$$

we can write an expression for the rate of change of the body temperature.

$$\frac{dT_B}{dt} = \frac{q}{M}(T_{IN} - T_{OUT}) + \frac{Q}{MC}$$

If a fish is without any mechanism to regulate the body temperature then $T_{out} = T_b$ and $T_{in} = T_a$. In that case the equilibrium body temperature excess will be

$$T_B - T_A = \frac{Q}{qC}$$

To estimate a numeric value for the present case we can use data for the metabolic rate of adult sockeye salmon, which is approximately 100 mg O_2 /kg/h (BRETT 1965). The cardiac output is estimated to be 40 ml/kg/min (WOOD and SHELTON 1980), which gives an expected temperature excess of 0.1 deg, or less if the heat flow through the skin is included in the model.

The same input data can be used to estimate the rate of change of the body temperature in

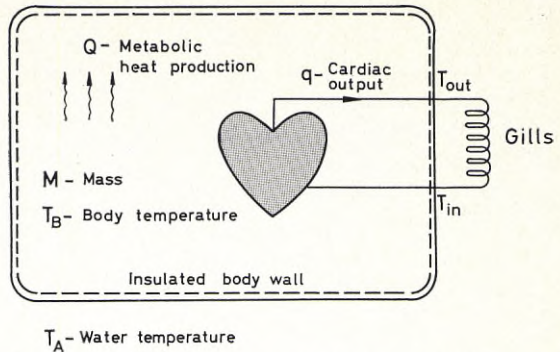


Fig. A 2. Simplified model of the thermal balance of a live fish.

two limiting cases of the model. First let us suppose that the ambient temperature changes suddenly by ΔT , and that this temperature change is large compared to the steady-state temperature excess before the change. Then, if the fish is without a heat-exchange system, we can write

$$\frac{dT_B}{dt} = \frac{q}{M} \Delta T$$

The other limiting case would be that the fish has a perfect heat exchanger at the gills, this means that $T_{in} = T_{out}$ and we have

$$\frac{dT_B}{dt} = \frac{Q}{C}$$

In the first case the initial rate of change will be $4 \cdot 10^{-2}$ deg/min times the magnitude of the temperature drop. In the second case there is a steady rise in body temperature which is approximately 6 mdeg/min.

If we compare the predictions from the model with the observations in Fig. A 1 it is seen that:

- 1) The steady-state temperature excess prior to the dive is 0.4 deg, which is significantly higher than that expected.
- 2) The initial rate of change after the 2.5 deg drop in ambient temperature is 0.07—0.08 deg/min, which is close to the expected 0.10 deg/min. But the temperature levels off abruptly after 2—3 minutes and remains constant at a level which is 0.2 deg below the initial temperature and approximately 3 deg higher than the surrounding water.

3) When the salmon re-enters the surface water the temperature starts rising towards the earlier steady-state level. This rise is slow and essentially linear, with a magnitude of 5.6 mdeg/min, which compares well with the estimated rate if the salmon can preserve all the metabolic heat.

Observations 1) and 3) give an indication that the salmon has a system for thermoregulation. 2) is more enigmatic. The regulating system may have a slow response, or there is the possibility that the viscera are protected against a transient temperature change in the body by a change in the blood circulation.

Reports from the Institute of Freshwater Research, Drottningholm

- *1. *Gunnar Alm.* Statens undersöknings- och försöksanstalt för sötvattensfisket. Dess tillkomst, utrustning och verksamhet. English summary. 1933. Pris kr. 0: 75.
- *2. *Gunnar Alm.* Vätterns röding, Fiskeribiologiska undersökningar. Deutsche Zusammenfassung. 1934. Pris kr. 0: 75.
- *3. *Christian Hessle.* Märkningsförsök med gädda i Östergötlands skärgård åren 1928 och 1930. English summary. 1934. Pris kr. 0: 50.
4. *Gottfrid Arvidsson.* Märkning av laxöring i Vättern. Deutsche Zusammenfassung 1935. Pris kr. 0: 75.
- *5. *Sten Vallin.* Cellulosafabrikerna och fisket. Experimentella undersökningar. Deutsche Zusammenfassung. 1935. Pris kr. 0: 75.
- *6. *Gunnar Alm.* Plötsliga temperaturväxlingars inverkan på fiskar. Deutsche Zusammenfassung. 1935. Pris kr. 0: 75.
- *7. *Christian Hessle.* Gotlands havslaxöring. English summary. 1935. Pris kr. 0: 75.
- *8. *Orvar Nybelin.* Untersuchungen über den bei Fischen krankheitserregenden Spaltpilz *Vibrio Anguillarum*. 1935. Pris kr. 1: 25.
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