SWEDISH BOARD OF FISHERIES

INSTITUTE OF FRESHWATER RESEARCH

DROTTNINGHOLM

Report No 58

LUND 1979
BLOMS BOKTRYCKERI AB

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Contents

Home Range, Migrations and Orientation Mechanisms of the River Indalsälven Trout, *Salmo trutta* L.

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CONTENTS

I. INTRODUCTION

The Baltic trout (*Salmo trutta* L.) is an anadromous species. It spawns in rivers and migrates to the sea where it spends most of its adult life. Like the Baltic salmon (*Salmo salar* L.) but contrary to the Pacific salmon species (BRETT and GROOT 1963, HARDEN-JONES 1968) the trout may spawn several times. The juveniles leave the river as smolts. In the northern part of the Baltic the trout, unlike the salmon, do not migrate far into the sea. Salmon from northern Swedish rivers have their feeding areas in the southern Baltic (CARLIN 1968) whereas most of the trout from the same rivers move only to feeding areas within about 200 km from the river mouth (CARLIN 1965).

It is a well-known fact that Baltic salmon and trout have strong homing instincts and abilities. This makes them suitable for studies on the orientation mechanism. Such studies were started at the Department of Ecological Zoology, Umeå in 1968. Two reports on salmon were published (BERTMAR and TOFT 1969, TOFT 1975). Beside the field work, the structure of the olfactory organs of trout has been studied by means of light- and electron-microscopy techniques. These studies have given a detailed picture of the trout olfactory organs on different structural levels (BERTMAR 1972 a—d, BERTMAR 1973, BERTMAR 1978).

The salmon stocks have been more intensively studied than have those of the trout. CHRISTENSEN and JOHANSSON (1975) have collected references on salmon studies from Denmark, Finland, Germany, Poland, U.S.S.R. and Sweden. There is, however, a growing interest in management of the trout stocks and it should be remembered that results from studies on salmon are not always valid also for trout. There is also some evidence that there may be differences between various local stocks of the same species (LARSSON 1977).

II. MATERIAL AND METHODS

Fish

All of the 538 trout were caught close to the Bergeforsen rearing plant, north of Sundsvall (Figs. 1, 2). They belonged to the River Indalsälven stock and were of two different categories (Table 1).

Subadults (barren trout): immature trout homing after only one year in the sea. In all 338 subadult trout were used for the experiments. Subadults and grilse represent a large but varying part of the trout and salmon stocks, respectively. They are not used for breeding and are not for sale after September 1. It was therefore possible to use some of them for experiments. The subadults were caught when homing in the autumn. They were then handled and released in a few days. Tagging experiments have shown that they return again, often within a few days (SAHLIN, pers. comm.). They therefore represent an almost optimal material for testing homing orientation mechanisms.

Adults: mature trout, homing after 2—4 years in the sea, stripped and used for breeding at the Bergeforsen rearing plant. They are bigger than the subadults, and their return migration for spawning usually takes place earlier in the summer. Altogether 200 adult trout were used.

Most fish were caught in the central fishery

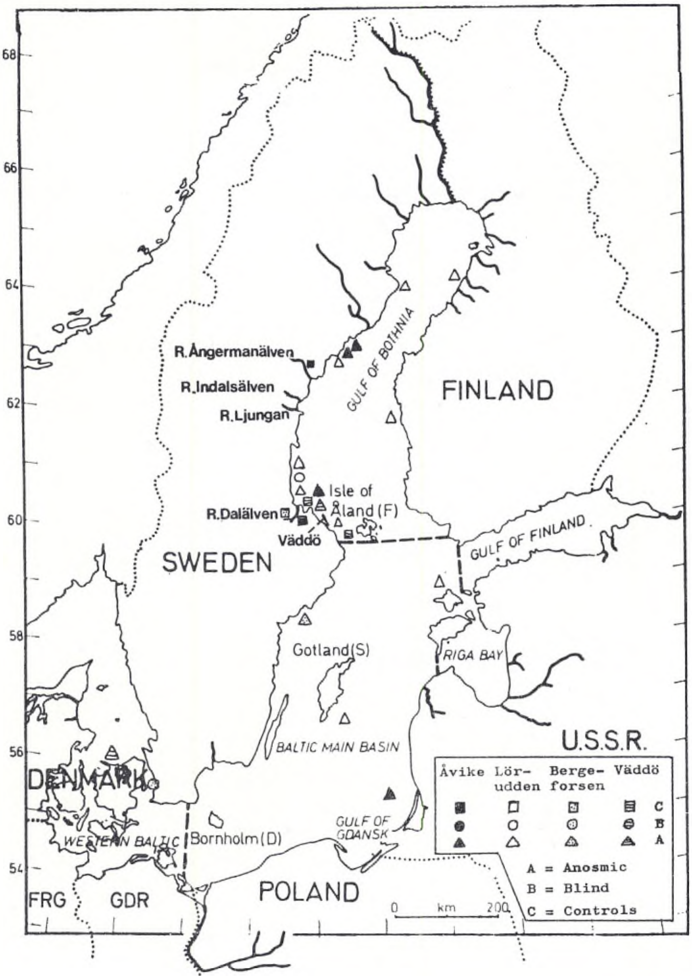

Fig 1. The Baltic area. Rivers and river streches still supporting salmon and sea trout runs. Recaptures of tagged River Indalsälven trout outside their home range.

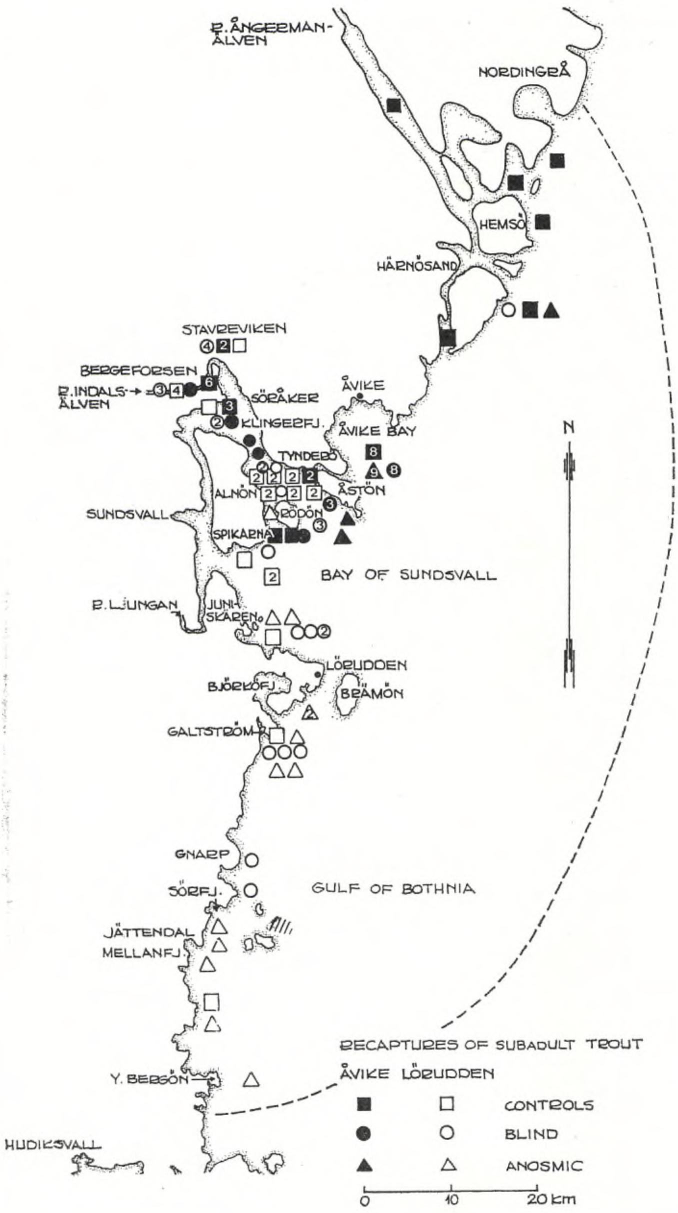

Fig. 2. Geographical distribution of recaptured tagged subadult trout, released at Åvike and Lörudden Oct. 1968. Home range indicated by broken line.

trap at the power dam, and 50 trout were caught by seine in the river at the Bergeforsen plant.

Home range and homing

Home range may be defined as the area over which an animal normally travels (GUNNING 1963). In this study the term is used for the area in which all animals of a population migrate.

Homing has been defined as the return of a fish to a home range following experimental or natural displacement (GUNNING 1963). The term has also been used in other ways but usually without clear definition. Fishery biologists seem to use the term for the return of a fish to the home river. Others use it in an even more restricted way to designate the return of fish to the home river but only during their spawning migration. The differences in definition seem to reflect the differences in fish material, home range

Table 1. *Fish material and release sites for field experiments with sea trout*

	Fish stock					Released		
Serial nr	Tag no.	Category	Exp. group	n	Date	Site	Code	Distance
C 68 40 02 0	S 525600— S 525649	Subadults	Controls	50	Oct. 21, 1968	Åvike	245	45—60 km
C 68 40 04 0	S 525500— S 525549	Do.	Totally anosmic	48	Do.	Do.	Do.	Do.
C 68 40 06 0	S 525550— S 525599	Do.	Blinded	47	Do.	Do.	Do.	Do.
C 68 42 02 0	S 525750— S 525789	Do.	Controls	40	Do.	Lörudden	247	50 km
C 68 42 04 0	S 525650— S 525699	Do.	Totally anosmic	50	Do.	Do.	Do.	Do.
C 68 42 06 0	S 525700— S 525749	Do.	Blinded	50	Do.	Do.	Do.	Do.
	Sö 26700— Sö 267029	Do.	Totally anosmic	24	Nov. 11, 1976	Grisslehamn (Väddö)	264	240 km
	Sö 267045— Sö 267049	Do.	Do.	5	Do.	Do.	Do.	Do.
	Sö 267030— Sö 267044	Do.	Controls	14	Do.	Do.	Do.	Do.
	Sö 267050— Sö 267059	Do.		10	Do.	Do.	Do.	Do.
C 70 40 02 0	S 822650— S 822699	Adults	Controls	50	Nov. 10, 1970	Bergeforsen	040	0 km
C 70 40 04 0	S 822600— S 822649	Do.	Totally anosmic	50	Do.	Do.	Do.	Do.
C 70 40 06 0	S 822700— S 822749	Do.	Blinded	50	Do.	Do.	Do.	Do.
C 70 40 08 0	S 822750— S 822799	Do.	Partly anosmic	50	Do.	Do.	Do.	Do.

and migration pattern. In this study, the term is used for the return of fish, at any time, to their home river or river mouth.

Tagging experiments have shown that most trout from the River Indalsälven are recaptured 20—50 km, and a few within 100—200 km from the river mouth (LUNDIN 1976).

Experimental technique

In 1967—68 the author initiated techniques for severing the olfactory nerves (neurotomy) and cauterization (burning) of the olfactory organs in salmon and trout. These techniques were later described (BERTMAR and TOFT 1969), and the cautery technique was also used on trout in 1968 and 1970. Altogether 177 trout were made anosmic by bilateral cauterization of the olfactory organs, and 50 were made partly anosmic by unilateral cauterization of the right olfactory organ. As the trout material was restricted, the neurotomy technique was excluded, cauterization being easier, faster and more effective and permanent. It eliminates the sensory cell bodies and therefore gives no chance for the olfactory nerve to regenerate. Neurotomized fish (with intact olfactory organs), on the other hand, can regenerate the olfactory nerve and therefore the fish might be able to use the organ again.

Impairment of vision was also performed with the U-formed nib of the soldering copper used for cautery of the olfactory organs. The difference was that not the whole organ was destroyed. By a touch of the nib the cornea was coagulated and made opaque.

After operation the fish recovered in running water for 3—6 days in 5×5 m basins within the river.

No traumatized trout were used, as the traumatized grilse salmon of 1967 did not show significant differences from intact controls (BERTMAR and TOFT 1969). Only completely intact fish, therefore, were used as controls in the trout experiments.

The numbers of trout of different experimental groups are given in Table 1.

Handling and transport

The essentials as regards catch technique, anaesthesia, tagging and rehabilitation were the same as for the grilse described earlier (Bertmar and Toft 1969, Toft 1975).

The subadults were weighed, measured (total length) and tagged. In all 224 trout were operated and released, and 114 were controls. The 200 adult trout were measured and tagged, and 150 of them were operated on and released. The adults were not weighed at release, but the sex was determined.

The mortality was low. Two anosmic and three blinded subadults did not recover in 1968, and six anosmic and one control subadult trout died in 1970, probably because of injuries from the net (Åslin, pers.comm.).

No fish died during the transportation, and all were in good condition when released. The transportation to Grisslehamn took about 7 hours. The fish were calm and remained close to the bottom of the tank. The temperature in the tank was then 3.0°C, in the river 0.8°C and in the sea 2.5°C. There was no wind at release. When released the fish dived and rapidly disappeared.

Release sites

The sea trout were released at different times and places inside and outside the home range (Table 1). These sites were chosen according to the orientation problems which were tested and in the ligth of earlier experience of the staff of the Bergeforsen plant.
The four release sites were the following.

1. Bergeforsen, at the salmon and trout rearing plant, about 15 km from the mouth of the Indalsälven river (Fig. 2). The estuary below is named the Bay of Sundsvall.
2. Åvike, situated at the north coast of the Åvike Bay, north of the Bay of Sundsvall. In order to return from this site the fish had to travel 45—60 km (north or south of the isle of Åstön).
3. Lörudden (Löran), immediately south of the Bay of Sundsvall. The trout had to pass the mouth of the River Ljungan in order to reach the home river.
4. Grisslehamn, on the northern coast of the Väddö Island (Fig. 3). This site is outside and south of the home range for the Indalsälven trout. In order to home from this site the trout had to pass the mouth of several rivers.

Recapture categories

The fish recaptured at the Bergeforsen rearing plant were, as before, caught in the central fishery trap or by seine. The rest were recaptured by commercial fishermen or anglers. The fishing methods differed, and a certain loss from non-reported recaptures can not be avoided. The same deficiences are also valid for the tagging experiments performed by the Swedish Salmon Research Institute (Carlin 1971), the results of which are used for comparison in this paper.

The recaptured fish have been grouped in the following categories.

1. Minus trout, fish caught at the release sites. These 14 fish were all subadults. They have

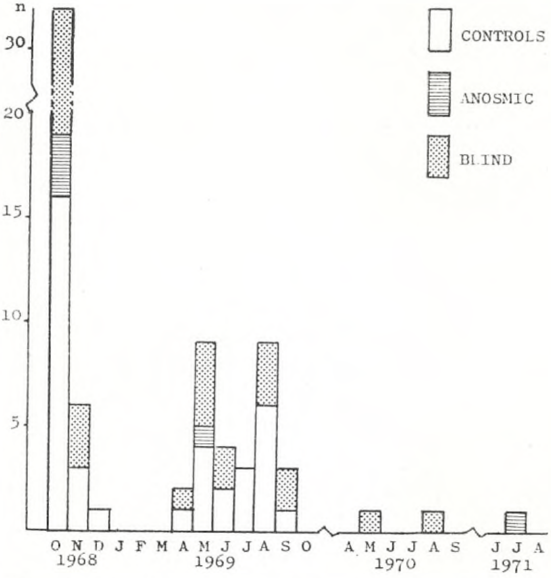

Fig. 3. Monthly recaptures of tagged experimental trout. Homing subadults.

been excluded before the statistical analysis was made.

2. Homers, trout recaptured in the Indalsälven river and the Bay of Sundsvall. The latter is the estuary of both the home river and the Ljungan river, but as there are no recaptures in the latter river it is presumed that all trout recaptured in the Bay actually were homers.
3. Stayers, trout caught in the home range but not as homers or minus trout.
4. Strayers, trout recaptured outside the home range.

Data processing

The Swedish Salmon Research Institute uses automatic data processing (Carlin 1971). This system was also used in this study. The same sort of tags (Carlin tags) were used as by the Salmon Research Institute and the Institute of Freshwater Research, Drottningholm (Table 1).

The results have been statistically analysed with 95 per cent confidence limits at the binomial distribution.

III. RESULTS

Tests of operation technique

The effect of cauterization of the olfactory organs was tested in trout smolts. At the Norrfors rearing plant (River Umeälven), five fish were anaesthesized and operated on in the same way as the adult trout used in the field experiments, except that as the fish were smaller, a soldering copper with a smaller nib had to be used. The fish were then tagged and, together with five controls, put back into the tank. A recovery period of about 45 min. was enough for them to again behave normally. The fish were then studied during two weeks with regard to their swimming, feeding, schooling and general behaviour. During this period there were no differences observed between the operated fish, the tagged controls and the intact fish.

The operated fish were then moved to an aquarium at the University of Umeå and kept for two years in running tap water in order to study the healing process after the operation. The fish behaved normally in the aquarium also. The two holes in the nose gradually decreased in size, and in 2—3 months a new single nostril formed on each side of the nose. This indicated that water circulated in the nasal cavities.

Every fifth month a fish was killed and the entire nose was fixed in Bouin's picrin-formaldehyde solution. After paraffin embedding and sectioning, the material was stained with Azan-Mallory. Further information on the histological technique is given elsewhere (Bertmar 1972 c).

The histological analysis showed that in three fish the operation had damaged all the olfactory rosettes. Only a large nasal cavity and a nasal sac were left on each side. The nasal sacs had a very thick and stratified cuboidal epithelium with numerous mucous cells, indicating that the nasal cavities were filled with mucus, when the fish were alive.

In the last two fish some parts of the olfactory rosettes were left. The remaining part of the olfactory organ was of about the same structure as in the three fish mentioned above. As in these, there was scar tissue around the nasal sacs and especially in the walls of the new, secondary nostrils, but not inside the nasal sacs.

From these tests it can be concluded that the operation technique was suitable for field experiments, at least as regards survival, feeding and other normal behaviour of the trout. But it is essential that the soldering copper should be big enough and that, after penetrating the nasal bridge and the two nostrils on each side, it should be properly circulated within the olfactory cavity for about 10 seconds to ensure that no olfactory epithelium remains. Then the coagulated olfactory organ should be lifted out.

Subadult trout released within the home range

The control fish were of the same stock and age as the operated fish. They are therefore of importance for estimating the normal home range of the population studied. It appeared that the controls stayed within 50 km from the site of release (Figs. 2, 6). Fig. 1 shows that only one control and one blind subadult strayed out of the home range (northwards up to the Ångermanälven

Table 2. *Number and weight of recaptured subadults released inside the home range*
Released Oct. 21, 1968 on the coast

	Experim.	Release	Homers				Stayers				Strayers				Total			
n	group	site	n	%[1]	$\overline{w}$	$\overline{\overline{w}}$	n	%[1]	$\overline{w}$	$\overline{\overline{w}}$	n	%[1]	$\overline{w}$	$\overline{\overline{w}}$	n	%[2]	$\overline{w}$	$\overline{\overline{w}}$
90	Controls	Åvike	15		1.4	0.3	13		1.1	0	1		1.0	0.4	29		1.2	0.2
		Lörudden	22		2.2	0.2	2		1.8	0	0				24		2.0	0.1
		Total	37	69.8	1.8	0.3	15	28.3	1.5	0	1	1.9	1.0	0.4	53	58.9	1.6	0.15
98	Anosmic	Åvike	2		2.8	2.0	10		1.3	0.1	4		2.7	0.9	16		2.3	1.5
		Lörudden	3		1.0	0	10		1.3	—0.1	8		1.3	0	21		1.2	0
		Total	5	13.5	1.9	1.0	20	54.1	1.3	0	12	32.4	2.0	0.9	37	37.8	1.8	0.8
97	Blind	Åvike	8		1.6	—0.1	8		1.3	0	0				16		1.5	—0.05
		Lörudden	22		1.6	0.1	6		1.5	0	1		1.7	0	29		1.6	0.05
		Total	30	66.7	1.6	0	14	31.1	1.4	0	1	2.2	1.7	0	45	46.4	1.55	0.0
285	Total	Åvike	25		1.9	0.7	31		1.2	0	5		1.9	0.7	61		1.5	0
		Lörudden	47		1.7	0.2	18		1.5	0	9		1.5	0	74		1.6	0
		Total	72	53.3	1.8	0.4	49	36.3	1.4	0	14	10.4	2.1	0.4	135	47.4	1.6	0.3

$\overline{w}$ Mean weight at recapture (in kg)
$\overline{\overline{w}}$ Mean weight difference between recapture and release weight (in kg)
[1] % of the total number of recaptured fish
[2] % of the total number of released fish

river and southwards down to the coast at Söderhamn). The 12 anosmic strayers were caught both north (Ulvöarna 3, Bjuröklubb 1, Pyhäjoki in N. Finland 1), east (Kristinestad in Finland 1) and south of the home range (Enångerviken south of Hudiksvall, Norrsundet at Gävle 1, Öregrundsgrepen 1, Dagö, Estonia 1, Gotland 1, Gulf of Gdansk 1, 800 km south of the home river). These trout had completely lost their orientation ability, and many of them moved far out of their home range.

A comparison of the release sites shows (Table 2) that significantly more controls from Åvike stayed than did those from Lörudden, and that more blind trout homed from Lörudden than from Åvike. The first difference may partly be due to the more intensive fishing in Åvike Bay, and to the fact that the released trout presumably had greater difficulty in orientating out of a bay. The reason why more blind trout homed from Lörudden may be that most river water turns south when leaving the Bay of Sundsvall (LINDROTH 1953), and therefore the trout released south of that bay found it easier to compensate for the blindness by olfactory orientation upstream and back to the home river.

The recaptures of blind trout were about the same as for controls (Table 2). Of the released blind fish 46.4 per cent were recaptured, of these only 2.2 per cent strayed and 31.1 per cent stayed, but 66.7 per cent homed.

Of the anosmic fish 37.8 per cent were recaptured, but these showed quite a different behaviour from the controls and also the blind trout. Only 13.5 per cent of the recaptured anosmic trout homed, but as much as 54.1 per cent stayed and 32.4 per cent strayed. Not a single anosmic trout returned to the home river (Table 7).

These significant differences show that the subadult trout mainly used their olfactory organs, not vision, for their orientation back.

Recaptured operated trout were of about the same weight as the recaptured control fish (Table 2). Neither anosmic nor blind trout had lost weight. On the contrary, the total mean weight difference between recapture and release weight was +0.3 kg. It can therefore be concluded that the operated trout must have eaten and grown normally.

The recaptured males were somewhat bigger than the females (Table 3). The sex was not recorded in all recaptured subadults.

Of the 38 subadults homing in 1968, 82 per cent were recaptured in October a few days after release (Fig. 3). Their homing drive was therefore not disturbed by handling and operating the fish.

In 1969 the homers had a periodicity (Fig. 3) which probably reflects a rhythm in their migra-

Table 3. *Number and weight of recaptured female and male trout*

Experim. group	Subadults				Adults			
	♂		♀		♂		♀	
	n	w̄	n	w̄	n	w̄	n	w̄
Controls	12	1.4	15	1.9	4	6.6	20	3.5
Totally anosmic	4	2.5	10	1.2	11	4.7	16	3.6
Blind	18	1.8	11	1.6	14	3.3	5	2.8
Partly anosmic					8	3.8	17	4.0
Total	34	1.9	36	1.6	36	4.6	59	3.5

w̄ Mean weight at recapture (in kg)

tory behaviour, whereas in 1970—72 the recaptures were too few to show a rhythm. The latter recaptures were operated fish, a fact which may indicate a tendency for these fish to be delayed in their homing run.

The strayers showed a similar rhythm in 1968—70 (Fig. 4). In 1971—72 only trout, released outside the home range, were recaptured.

Most stayers were recaptured within a few weeks (Fig. 5). There was no periodicity in the recaptures, but in 1969 all stayers were caught in summer. This is a difference compared to the homers and the strayers.

Subadult trout released outside the home range

Only one trout homed of the 53 released at Grisslehamn (Table 4). This control fish was recaptured in August 1971. In the same month another intact trout was caught at Iggön near Gävle, and in February 1972 a further one was recovered at Älvkarleby in the River Dalälven. These two trout had moved to the north and may therefore have been potential homers. One control trout was caught at Åland, south of the release site.

Of the anosmic trout, one was recaptured at Singö after 15 days, and another strayed to Kattegatt. It was recaptured at Sjaellands Udde, Denmark, in April 1972. No anosmic trout was recaptured north of the release site.

Adult trout

The adult trout were released in the River Indalsälven and thus within the home range. The recaptures of the control trout show that the home range was smaller in the north than that of the subadults (Fig. 6).

Only a few adults strayed. One control, one totally anosmic and one partly anosmic trout swam to the periphery of the home range (Fig. 6).

Of the 200 released adults, 49 per cent were recaptured; 80.6 per cent of the recaptures were homers, but only 13.3 per cent stayed and 6.1 per cent strayed outside the home range (Table 5).

Of the totally anosmic trout, 75 per cent were homers. Of these, 36 per cent were caught in the home river, whereas 30 per cent of the partly anosmic trout and 20 per cent of the controls were recaptured in the home river (Table 7). Not a single blind fish was recaptured in the home

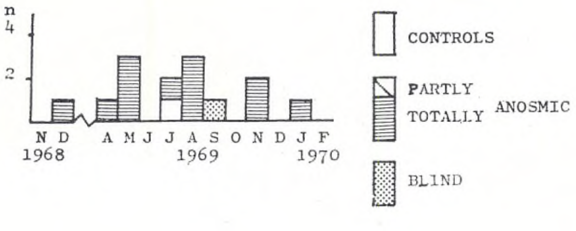

Fig. 4. Monthly recaptures of tagged experimental trout. Straying subadults.

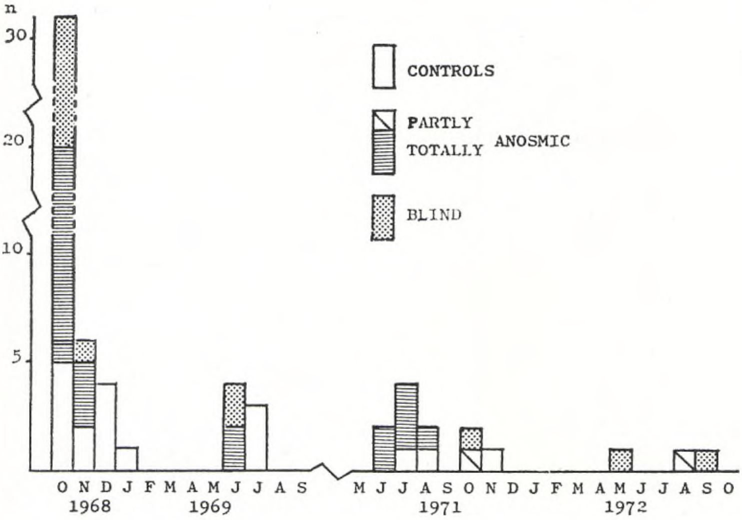

Fig. 5. Monthly recaptures of tagged experimental trout. Staying subadults (1968—69) and adults (1971—72).

river, but as many as 14 (73.7 per cent) were caught in the estuary (Fig. 6).

The mean weight at recapture and the mean total length at release were 4.1 kg and 65 cm, respectively (Table 5). These fish were therefore considerably bigger than the subadult trout, the weight and length of which were 1.6 kg and 47 cm, respectively. Three female and four male adults weighed about 7 kg. The biggest fish was a male control trout of 8.5 kg. Between release and recapture (10 months) it grew from 71 cm to 83 cm, total length. It was recaptured during a subsequent spawning run in the river mouth. A female anosmic trout of 7.2 kg grew from 70 cm to 84 cm in 32 months.

As in the subadults, there were no significant differences in length and weight between recaptured control and operated adult trout (Table 5). The operated fish may therefore have eaten and grown normally.

Nor were there significant differences in sex ratio between homers, strayers and stayers (Table 6). Except for blind trout the females were in a majority in the experimental groups. In all, 47.6 per cent of the males and 50 per cent of the females were recaptured. Of the anosmic males 78.6 per cent were recaptured, compared with 47.2 per cent of the anosmic females. But only 35.9 per cent of the blind males were found, compared with 45.5 per cent of the blind females. The controls showed about the same relation between males and females as in the blind fish. The sex ratio of recaptured partly anosmic trout was normal.

In 1971 the homing migration of the adults showed peaks similar to that of the subadults in

Table 4. *Number of recaptured subadults released at Grisslehamn (Väddö), outside the home range.*

Released Nov. 11, 1970 outside home range		Recaptured							
	Experim.	Homers		Stayers		Strayers		Total	
n	group	n	%[1]	n	%[1]	n	%[1]	n	%[2]
24	Controls	1	25.0	0		3	75.0	4	16.7
29	Anosmic	0		1	50.0	1	50.0	2	6.9
53	Total	1	16.7	1	16.7	4	66.6	6	11.3

[1] % of the total number of recaptured fish

[2] % of the total number of released fish

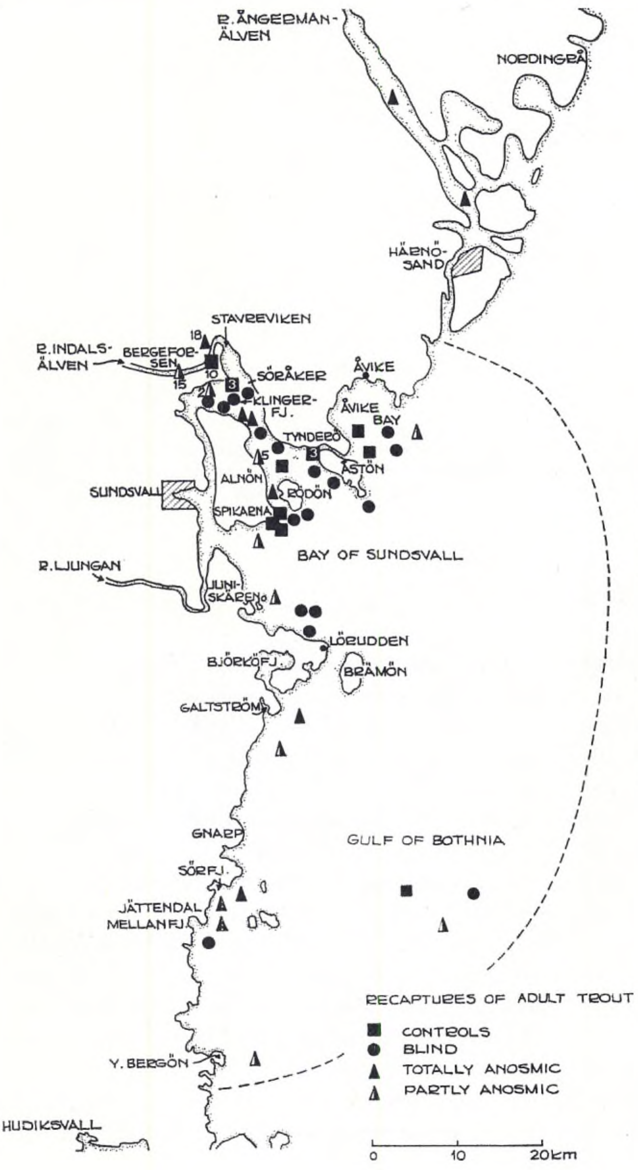

Fig. 6. Geographical distribution of recaptured tagged adult trout, released at Bergeforsen and found within the home range (broken line).

spring and autumn (Fig. 7). A rudimentary homing rhythm also occurred in 1972, whereas in 1973—74 the recaptures were too few to show the pattern.

Both controls and operated fish have this rhythm in homing.

The recaptures of staying and straying adult trout were too few to show a rhythm (Figs. 4, 5).

IV. DISCUSSION

Ecological factors and survival of the trout

The local stocks of Baltic trout and salmon differ in growth and migration behaviour (LARSSON 1977, STEFFNER 1977). These differences are inherited. In the first place comparisons are therefore made with earlier tagging experiments on

Table 5. *Number, weight and length of recaptured adults released at Bergeforsen (home river).*

Released Nov. 10, 1970 in home river		Homers				Stayers				Strayers				Total			
n	Experim. group	n	%[1])	$\bar{w}$	$\bar{L}$	n	%[1])	$\bar{w}$	$\bar{L}$	n	%[1])	$\bar{w}$	$\bar{L}$	n	%[2])	$\bar{w}$	$\bar{L}$
50	Controls	20	83.3	4.2	62	3	6.0	4.6	67	1	2.0	2.4	51	24	48.0	3.7	60
50	Partly anosmic	24	88.9	3.5	63	2	7.4	4.3	61	1	3.7	4.2	66	27	54.0	4.0	63
50	Totally anosmic	21	75.0	4.7	66	4	14.3	3.9	66	3	10.7	5.5	66	28	56.0	4.7	66
50	Blind	14	73.7	2.7	67	4	15.8	4.0	68	1	10.5	3.0	75	19	38.0	3.2	70
200	Total	79	80.6	3.8	65	13	13.3	4.2	66	6	6.1	3.8	65	98	49.0	3.9	65

$\bar{w}$ Mean weight at recapture (in kg)
$\bar{L}$ Mean total length at recapture (in cm)
[1] % of the total number of recaptured fish
[2] % of the total number of released fish

the trout stock of the River Indalsälven. But more general comparisons are also made with other stocks and with other species.

The survival capacity is adapted to the ecological factors of the home river (Larsson 1977). Release of salmon and trout in strange waters may therefore have drastic effects on the survival.

The recaptures in the River Indalsälven of trout smolts released in their home river have varied between 8 per cent (in 1971 and 1973) and 32 per cent in 1960 (Sahlin 1977). The mean recaptures were 14.2 per cent. The trout of this study were recorded in the home river in a somewhat higher frequency: 14.4 per cent for subadults and 20 per cent for adults (Table 7). And if the river mouth is included, the recapture frequency was 43.3 per cent and 40 per cent, respectively (Tables 2, 6). Older fish therefore constitute a better material for homing experiments than smolts.

One reason for this difference in survival rate may be the size of the trout. In smolts larger size gives a higher frequency of recaptures (Svärdson 1966, Larsson 1977, Sahlin 1977, Steffner 1977).

There are also technical problems that may affect the work with trout. They have been described by Sahlin (1969). One of these is the tagging of the fish. A study of sea trout of the Verkeån river showed that many smolts lose their tags and have scars from lost tags (Svärdson and Anheden 1963). In this study, the handling, tagging, transport and operation of the adult trout had no significant effects on the recapture frequency. It is therefore obvious that adult fish are not as sensitive as juvenile fish.

Table 6. *Number of female and male adults recaptured inside and outside the home range.*

Released Nov. 10, 1970 in home river				Recaptured															
				Home river and river mouth				On the coast inside home range				Outside home range				Total			
				♂		♀		♂		♀		♂		♀		♂		♀	
n	Experim. group	♂	♀	n	%[1])	n	%[1])	n	%[1])	n	%[1])	n	%[1])	n	%[1])	n	%[2])	n	%[2])
50	Controls	11	39	4	100	16	80	0		3	15	0		1	5	4	36.4	20	51.3
50	Partly anosmic	20	30	11	100	13	81.3	0		2	12.5	0		1	6.2	11	55.0	16	53.3
50	Totally anosmic	14	36	8	72.7	13	76.5	2	18.2	3	17.6	1	9.1	1	5.9	11	78.6	17	47.2
50	Blind	39	11	9	64.3	5	100	4	28.6	0		1	7.1	0		14	35.9	5	45.5
200	Total	84	116	32	80.0	47	81.0	6	15.0	8	13.8	2	5.0	3	5.2	40	47.6	58	50.0

[1] % of the total number of recaptured fish
[2] % of the total number of released fish

Table 7. *Sea trout and salmon grilse of the Indal stock recaptured as homers in the River Indalsälven. Grilse are from field experiments in 1967—68 (Toft, 1975).*

Experimental group	Number of released			Homers in home river					
	sub-adults	adults	Salmon grilse	sub-adults		adults		salmon grilse	
				n	%	n	%	n	%
Controls	90	50	574	13	14.4	10	20.0	70	12.2
Partly anosmic		50				15	30.0		
Totally anosmic	98	50	554	0	0	18	36.0	20	3.6
Blind	97	50	75	8	8.25	0	0	13	17.3
Total	285	200	1203	21	7.4	43	21.5	103	8.6

The trout were caught, handled and tagged by the same personnel as in earlier tagging experiments with trout smolt. It is therefore reasonable to disregard technical factors when comparing the results of the experiments with smolt and older trout.

The survival of the trout may also depend on the presence of food and predators (Svärdson 1966). Bams (1967) studied different categories of sockey salmon migrant fry which were exposed to predation tests. These showed the importance of size for the survival of the fish. Preliminary experiments have shown that it is possible to increase the survival of salmon smolt by conditioning against predators immediately before release (Larsson 1977).

Trout smolt of the Indalsälven river are preyed on by pike, perch and burbot. But adult trout of the size used in this study probably have rather few predators. It is possible, however, that subadults suffer a higher predation than the adult trout. This could partly explain the lower percentage of recaptures of the subadults (Table 7).

The time of release may influence the results. In trout smolt, release during spring (May) seems to be the most favourable (Larsson 1977, Steffner 1977). The trout of this study, however, were only available for experiments during autumn, and therefore no comparisons of release times have been made.

The position of the release site has sometimes been the decisive factor in comparative tagging experiments with smolt (Larsson 1977, Steffner 1977). There is a more extensive predation in the river than in the sea. But fish released in the sea and on the coast generally do not home as accurately as those released in the river. The trout of this study also homed in a higher frequency

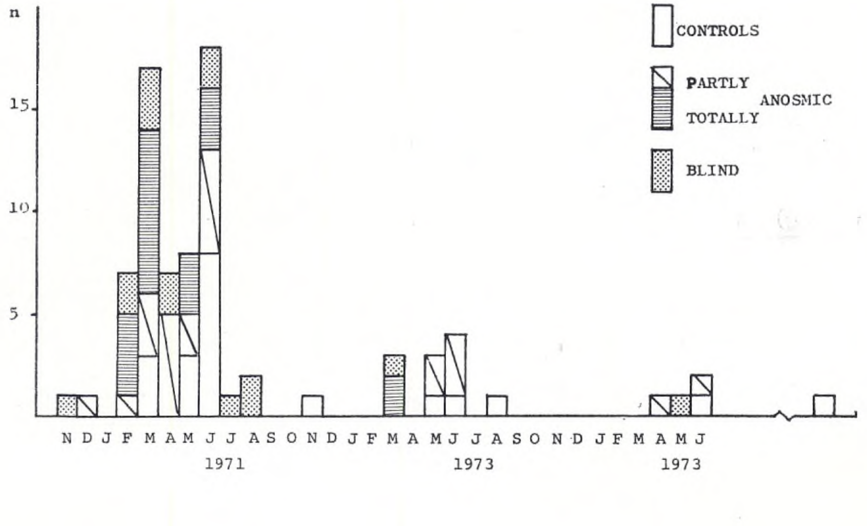

Fig. 7. Monthly recaptures of tagged experimental trout. Homing adults.

when released in the river (Table 2, 5). The age of the fish may, however, also be a contributary reason for this difference.

Various release sites may produce different recapture results due to differences in fishing intensity, geomorphology of the coast, position in relation to home river and to coastal currents. The temperature of the water at the release sites may be important for the survival and migratory behaviour of smolt (LARSSON 1977). In this study, the difference between the temperature of the transport tank and that of the release sites on the coast was only +0.5°C. The adult trout were released at the Bergeforsen rearing plant and they experienced no temperature differences.

The salinity may also affect the fish. Trout smolt are more sensitive to salinity differences than are salmon smolt during some parts of the year (LARSSON 1977). It is possible that salinity is a guiding factor for migrating trout. Both young and adult trout have in their olfactory organs labyrinth cells which are used to identify water of different salinity (BERTMAR 1972 d).

The final ecological factor to consider is the pollution of the water. Pollutants and the chemical senses of aquatic animals have recently been reviewed by SUTTERLIN (1974). There appears to be only limited evidence for direct damage by pollutants to chemoreceptor cells. No clear instances of masking of biological odours by pollutants have been demonstrated. Moderate avoidance by trout of bleach kraft mill effluent has been shown by SPRAGUE and DRURY (1969). But as we do have trout stocks in Swedish rivers polluted by pulp and paper mill effluents and other industries it is obvious that trout (and salmon) can home even in polluted water. One of the reasons for this important adaptation is that the olfactory organs of both juvenile and adult trout have cells which attack the bacteria and other pollutants that might infect the olfactory mucosa (BERTMAR 1973, 1978). Not only is the immune defence highly developed, however, but the olfactory mucosa of both juvenile and adult trout also has cells that take care of their own dead cells (BERTMAR 1973, 1978). So even if there is some damage by pollutants to the chemoreceptors, these cells can be phagocytized immediately and replaced by young olfactory receptor cells.

The olfactory organs in trout thus function optimally and are extremely well adapted for orientation during migrations.

Home range and migrations

GERKING (1959) listed 33 species and GUNNING (1963) four other fish species which exhibit restricted movements or occupy home ranges. Differences in sea distribution between stocks of trout and salmon have been reported by CARLIN (1965) and LARSSON (1977). The majority of the trout from rivers in Norrland released as smolt have been recaptured within 20 km from the river mouth, but a few have migrated 200 km or more. The stock of the Dalälven river has the largest home range of the rivers in Norrland (CARLIN 1965). Some of the trout may migrate up to Västerbotten or down to Skåne (Scania). And of the southern Swedish stocks that of the Verkeån river has an even larger home range (SVÄRDSON 1966), covering the whole southern Baltic basin.

There are, however, not only regional differences between the trout stocks but also intrapopulation variation (STEFFNER 1977). In some years all or most of the trout smolts stay near the estuary, in other years 10—23 per cent of them migrate 200 km or more (LUNDIN 1976). The present study has shown that there are also age differences (Figs. 2, 6). Trout released as adults stay within 50 km from the river mouth and rarely stray.

The recaptures plotted on the maps (Figs. 2, 6) indicate the following routes for experimental trout homing in the Bay of Sundsvall (Fig. 8). The fish head to the mouth of the Bay, then orientate towards Alnön, Rödön and Tynderö, pass between these islands and up to Klingerfjärden Bay, and finally reach the Indalsälven river. They do not pass the mouth of the Ljungan river, or to the west of Alnön. The Ljungan river has its own stock of trout and salmon and this study shows no straying of trout from the Indalsälven stock up into the Ljungan river, not even of operated fish. This constitutes a difference as compared with the Ångermanälven river stock, which runs north of and at a longer distance from the Indalsälven river (Figs. 2, 6).

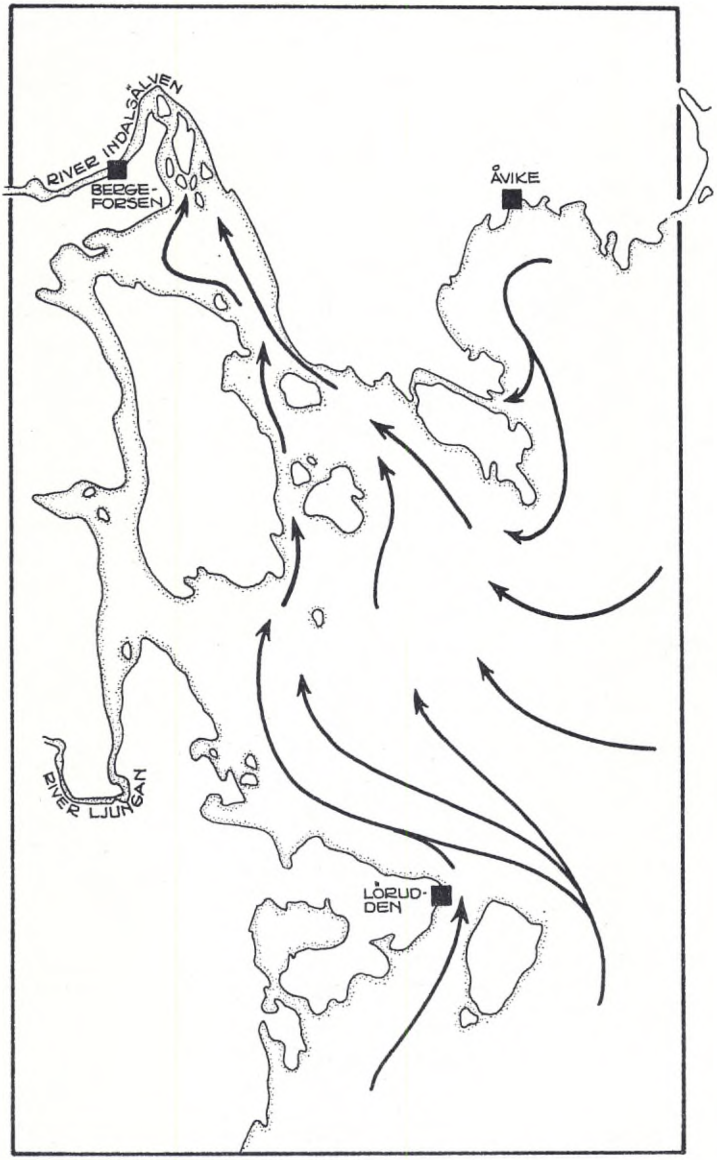

Fig. 8. Homing routes of sea trout of the River Indalsälven stock.

The movements of the subadults released south of the home range is difficult to determine, as the recaptures are few (Table 4).

For both categories of released trout there are migration rhythms (Figs. 3—5, 7). The results indicate that mainly in spring the trout migrate from the coast and into the Bay of Sundsvall and the Indalsälven river. In summer they usually stay within their feeding areas at the coast, and in autumn they perform the spawning migration. These spring and autumn migrations constitute different types of movements, and they can be considered as a type of diplochrone seasonal activity (two activity periods).

The high river water level in spring and autumn may influence the migration cycles. The trout smolt of the Verkeån river react very strongly to high water, and every rainfall usually starts a wave of migration the same or the following day (Svärdson 1966). It is well-known that ascending trout are stimulated by a rise of the water level. It seems that the rhythm of migration is an adaptation to the normal water fluctuation of the river.

It has been suggested that the homing instinct in trout is weaker than that of salmon (CARLIN 1965). But this is not valid for trout of the Indalsälven stock. There, 14.4 per cent and 20 per cent of the control subadults and adult fish, respectively, homed to the river as compared with 12.2 per cent of the salmon grilse (Table 7). The higher homing frequency in adults may be due to their maturity, experience and conditioning, but also to differences in release sites: the adults were released in the home river, the subadults on the coast.

Orientation mechanisms

Several techniques have been used to study the orientation of fish (KLEEREKOPER 1971, STASKO 1971). One of these is tagging/recapture of sensorily impaired fish. The only senses impaired in the studies in question have been vision and olfaction. The methods used to impair olfaction have been severing of olfactory nerves (neurotomy), cautery (burning) of the olfactory organ(s), or plugging of the nares with different substances. None of these studies, however, has sufficiently considered the time factor of the technique used, *i.e.* whether the operation gives a permanent or only a temporary impairment of the sensory organs. The reliability of the studies is therefore questionable. Cutting and plugging do not produce permanent impairment (STUART 1957) and cauterization can be incomplete (GUNNING 1959, LORZ and NORTHCOTE 1965). These measures should therefore be followed up by tests to determine their effectiveness. In spite of the fact that sensory impairment has been used in 15 studies since 1926, there have been no such tests on the same species used in the field experiment until recently, when this was done on Baltic salmon (TOFT 1975).

In the present study, long-term and detailed behavioural and histological tests were made to determine the effectiveness of the cautery technique and the possible influences on the normal behaviour. The anosmic trout of the field experiments were therefore effectively and permanently sensorily impaired.

No side effects were observed. These fish were still capable of distinguishing the chemical nature of food substances by taste, but they could not smell the water of the home river at any distance. Schooling of intact and operated fish was not observed.

The techniques used to impair vision have been surveyed by GUNNING (1959) and STASKO (1971). When blinding big fish like adult trout which have to be recaptured by fishermen or others than the scientific personnel, it was not possible to use eye caps, or any other method than cautery of the cornea. This method is fast and gives an opaque eye that can only register light differences. The diel activity is therefore probably normal in these fish.

Since both anosmic and blinded trout behaved and grew normally (Tables 2, 6), confident interpretation of the results from these tagging experiments with sensorily impaired trout is quite possible.

Ten tagging/recapture studies of sensorily impaired fish from the first experiment in 1926 up to 1971 show that olfaction plays a greater role than vision in homing to and within rivers (STASKO 1971). Three other studies show, however, that olfactory impairment had no effect on homing (PODDUBNY 1966, MCCLEAVE 1967, TESCH 1970). In one of these (MCCLEAVE 1967), continued homing may have been caused by a faulty occlusion technique.

Vision seems to play a secondary role, since in five out of eight studies blinded fish homed as accurately as the controls (GUNNING 1959, HIYAMA *et al.* 1966, MCCLEAVE 1967, JAHN 1969). But in the remaining three studies neither blinding nor olfactory impairment had any effect on the homing success (BARDACH 1958, LORZ and NORTHCOTE 1965, LABAR 1971). Combined blinding and olfactory impairment affected the fish most (LORZ and NORTHCOTE 1965, GUNNING 1959, GROOVES *et al.* 1968, JAHN 1969). TOFT (1975) discussed four hypotheses concerning the control mechanisms involved in the spawning migration of salmonid fish. The discussion is, however, based only on sensorily impaired grilse of two stocks of Baltic salmon, and no decisive theory is presented. Furthermore, the results are based only on the homing of these subadult salmon at spawning time. No other migrations of the year are concerned, and the home range has not been studied.

A preliminary study on grilse of the Indalsälven river shows that most bilaterally anosmic salmon stayed in the Bay of Sundsvall (22 per cent) or strayed (15 per cent), but only 4 per cent homed (BERTMAR and TOFT 1969). A later study on a larger series from that river and from the Skellefteälven river confirms these results (TOFT 1975). A comparison of homing grilse and trout of the Indalsälven stocks is given in Table 7. It excludes homers to the river mouth (Bay of Sundsvall), and shows that subadults are similar to the grilse but not to the adult trout: the subadults of both species did not home when blinded. Adults behaved in the opposite way: partly and totally anosmic trout homed as accurately as or even better than the controls, but blinded fish did not.

This means that the two salmonid species mainly orientate by chemotaxis when homing as subadults, whereas the fully mature fish mainly orientate by phototaxis during the movement in the home river. A species may thus use two different orientating mechanisms at different stages of their maturity.

Baltic salmon smolt are imprinted on the home river when leaving the estuary (CARLIN 1968). Similar imprinting probably occurs in Baltic trout smolt, but it seems that there also occurs imprinting upstream of the estuary. This study indicate that the imprinting is both olfactory (in the estuary) and visual (in the river). As smolt seem to stay a rather short time in the estuary, it appears that the olfactory imprinting is a rather rapid process. After that, if and when the trout leave the estuary, they seem to remember at least the olfactory cues on the way out to the feeding areas in the other parts of the home range. These cues may then be used as chemical guides during the migration back. In the first homing run, as immature subadults, most of the orientation movements from the feeding grounds to the estuary and the home river are then controlled by the olfactory memory. In later homing runs, as mature adult fish, the orientation to the home river is mainly controlled by the olfactory memory but within the river the migration is mainly controlled by the visual memory (Figs 2, 6).

The homing in grilse of Baltic salmon is also mainly guided by olfactory stimuli (Table 7), even when the fish are released on the eastern side of the Gulf of Bothnia at Vasa, Finland, more than 200 km east of the home river, the Skellefteälven (TOFT 1975). This means that they may home regardless of prevailing currents and salinity differences.

Recently it has been suggested by BODZNICK (1978) that the calcium level of the water may guide the sockeye salmon (*Oncorhynchus nerka*) home. This species can pick up calcium ions at well below naturally occurring concentration range, down to 5×10^{-6} molar. As a pointer some sockeyes were reared in Lake Washington water, and then run in a Y-shaped maze with their home-lake water in one arm and the same water with a tiny amount of calcium ions added in the other. All chose their unadulterated home water. In Baltic sea trout, the olfactory organs have a specialized cell type, so-called labyrinth cells, which may detect calcium (BERTMAR 1972 d). This may indicate that calcium is one factor working at the imprinting time, and that the calcium detector, the labyrinth cells, is one reason for the high homing capacity of Baltic sea trout.

It would be of the utmost theoretical and economic interest to know what kind of substances the fish are imprinted on at the river mouth and have learned to recognize in the sea. The river water may contain substances from the spawning sites or other biologically important parts of the river (HASLER 1966, HARA 1970, COOPER and HASLER 1974), and probably also pheromones (OSHIMA *et al.* 1969, DØVING *et al.* 1973, HÖGLUND and ÅSTRAND 1973, SOLOMON 1973, PFEIFFER 1974, NORDENG 1977), and predator and other interspecies odours (REED 1969, HÖGLUND *et al.* 1975, HARA and MACDONALD 1976) contribute to the imprinting.

Many of these and other papers on olfactory imprinting, electrophysiological approaches and chemical clues are summarized by HARA (1975). Later experiments with imprinting of coho salmon and rainbow trout on morpholine support the olfactory hypothesis of homing (COOPER and HASLER 1975, 1976, HASLER and COOPER 1976, Cooper and Scholz 1976, Cooper *et al.* 1976, Scholz *et al.* 1976).

Amino acids and related compounds, which are normally non-odorous to humans, seem to be one of the major active olfactory components in eliciting behavioural changes in many fish species (*cf.* Hara 1975). These acids might contribute to the effectiveness of food odours (Sutterlin 1975, Suzuki and Tucker 1971, Hara *et al.* 1973). This mechanism might then also have been used for orientation, and evolved into the navigation and homing capability.

The relative proportions of various amino acids distributed vertically and horizontally in oceanic waters differ (Pocklington 1972). If sea currents have different odours, such information could possibly be used in guiding fish.

Orientating processes are not always governed by strict stimulus-response relationships (von Holst 1950). The physiological condition of an organism exerts a decisive influence. The orientating reactions in trout are probably dependent upon readiness to act, such as the spawning drive. The relation between the olfactory sense and the reproductive cycle is known in mice (Bruce 1964), cats and other mammals. Pheromones have an effect on the oestrus cycle of individuals of the same species. There is structural and physiological evidence of connection between the olfactory lobe and the oestrus-controlling anterior parts of the hypothalamus in mammals (Ottoson 1970). In fish, plugging the nostrils or cauterizing the nasal epithelium in male gobiid fish (*Bathygobius soporator*) eliminated the courtship response, while increasing the tendency of male aggressive behaviour (Tavolga 1976). If there is such a relation in trout also, the gonads of the anosmic adult fish may have been affected by the operation, reducing the spawning drive and homing instinct. This may explain some of the results within this experimental group.

Finally, it has to be emphasized that there is an urgent need for an intensive and highly sophisticated chemo-analytical approach to the problem of odour identity of the waters of spawning grounds and migratory pathways (Kleerekoper 1976).

The stayers did not show the same olfactory or visual orientation as did the homers (Tables 2, 5). The adult stayers were not recaptured until several months after release, and most of them were recaptured during the spawning time (Fig. 5). But of the subadult trout, most of the stayers were like the homers, recaptured within a month (Fig. 5). This may indicate that they still had their drive intact, but had lost their homing mechanisms with the olfactory impairment. They may, however, have been able to compensate for the sensory impairment. Olfaction or vision was still undisturbed, and taste and latero-sensory organs were intact in all operated fish. There were no time differences between intact and impaired stayers (Fig. 5). This suggests that their normal behaviour was to stay in the home range or possibly to move more or less at random between feeding areas.

The number of straying fish increases if the trout smolt are released on the coast and not in their home river (Larsson 1977). This straying may be caused when the trout enter freshwater in order to stand the winter period better and utilize the nearest river.

Only two control trout strayed. Of these, one adult trout was caught in the Dalälven river in winter and one subadult was recaptured in the Ångermanälven river in summer. It is noticeable that no trout ran into the Ljungan river, even when the fish were released just south of that river (at Lörudden). It may be that when the trout have reached the Bay of Sundsvall, the homing drive is strong and the orientating mechanisms function optimally. The large pulp and paper mill effluent in the Ljungan river at the time of the experiments may also have repelled the trout. Sprague and Drury (1969) noted moderate avoidance by trout throughout the sublethal range of 10—100,000 ppm of bleach kraft mill effluent. Some indication of retarded movement and/or avoidance of the effluent from a pulp mill and other sources is also mentioned by Elson *et al.* (1972), who followed sonic-tagged Atlantic salmon through an estuary. Höglund (1961) introduced the fluviarium technique and observed avoidance by some species at a sublethal level of 0.1 ppm sulphide waste liquor, and he found anosmic fish incapable of avoiding sulphide waste liquor. He also demonstrated that the steepness of the gradient was an important cue

Table 8. *Orienting mechanisms, receptor organs and behaviour in sea trout.*

Main group of orienting mechanisms	Orienting receptor organs	Orientation behaviour	Age group
Orientation in fixed-space reference syst.: Stimulus sources provide the coordinates and/or serve to maintain the normal position, and they are not the goal of the orientation	Gravity and proprioceptive organs	Maintenance of physical balance	Subadults and adults
		Control of position and direction of action in space	Do.
	Eyes	Orientation related to light	Do.
		Horisontal near-orientation to landmarks	Do.
	Latero-sensory organs	Tactile, kinesthetic registration and repetition of the own movements	Do.
		Orientation in currents	Do.
Stabilization of posture and movement (locomotion) independent of locality	Semicircular canals and utriculus-sacculus (inner ear)	Orientation related to equilibrium	Do.
	Eyes	Optomotoric (kinetic) control	Do.
Object orientation: Stimulus sources are the objects of orientation; frequently locating processes (goal and direction is considered)	Eyes	Optical target orientation	Do.
	Lagena (inner ear)	Acoustical orientation	Adults in home river
	Skin receptors	Tactile orientation to other fish etc.	Subadults and adults
			Do.
	Gustatory receptors	Chemosensory near-orientation to food etc.	Do.
	Olfactory organs	Chemosensory near-orientation to different water qualities in feeding areas	Do.
		Homing orientation	Adults up to the estuary, subadults all the way

in the animal's ability to avoid toxic levels. It seems as if anosmic trout, too, avoided the sulphide waste liquor in the mouth of the Ljungan river, but their taste sense (and vision) might have been still intact.

In general, most trout strayers were anosmic, not blind. And most strayers were subadult (Fig. 1, Tables 2, 5). As the homing orientation in the subadult trout was mainly guided by olfactory stimuli, it appears that compensatory orientation by means of other senses and brain centra was impossible, and they therefore strayed. Mature adults, on the other hand, had a longer experience and they could usually adapt to the sensory impairment. Consequently, very few of them strayed.

The orientation mechanisms of the subadults released outside the home range usually did not guide the fish back. The only certain exception has a control fish caught in Klingerfjärden, Bay of Sundsvall, having travelled about 240 km in nine months at sea. The results indicate (Table 4) that most displaced trout strayed, probably because the innate orientating mechanisms did not function outside the home range.

Salmon grilse of the Indalsälven stock were also released at Väddö, but these, too, did not show significant differences between homers and strayers or between anosmic and control fish (Toft 1975). This is a difference as compared with the grilse released at Vasa, about the same distance to the east of the home river. No explanation has been given, but one reason may be the influence of different release sites discussed above.

There are also other receptor organs for orientation in trout, but they have not yet been studied in field experiments.

The most important receptor organs in adult trout are correlated with the main groups of

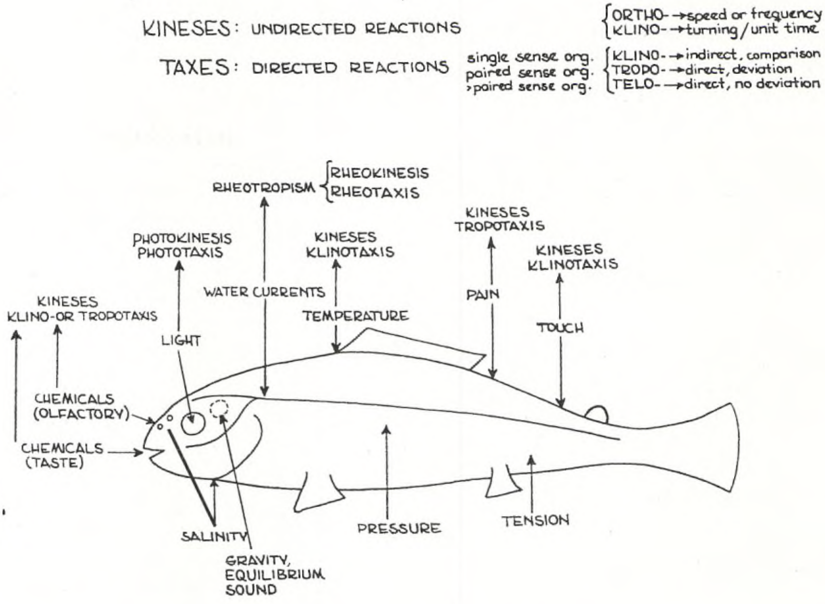

Fig. 9. The main reactions and stimuli that may be involved in sea trout orientation behaviour.

orientating mechanisms summarized in Table 8. These mechanisms are classified according to their function. They are modified from SCHÖNE (1965) and EIBL-EIBESFELDT (1970). These types of orientation behaviour are probably present in adult sea trout, but not always in the same area or season of the year. The subadults mainly used olfaction for homing orientation, and the adults mainly used vision for the same kind of orientation in the river, for example.

The orientation behaviour is sometimes described in terms such as kineses (undirected reactions), taxes (directed reactions) and their subterms. The main reactions and the stimuli that release them in sea trout are shown in Fig. 9. Klinotaxis and tropotaxis are also used in olfactory orientation. They start with chemicals (ions and molecules) that circulate in the paired olfactory organs, and they release a chain of directed reactions that end with orientation to another place where other chemical stimuli are present.

V. SUMMARY

538 Baltic trout (*Salmo trutta* L.) of the River Indalsälven stock were studied by means of field experiments. Behavioural and histological tests were used to control the efficiency and permanence of the operation techniques. Olfactory or visual impairment was effected by cauterization. Operated fish together with intact controls were released in the home river, on the coast south and north of the river mouth (the Bay of Sundsvall) and at the isle Väddö south of the home range. In their homing the subadult immature fish were mainly guided by olfactory stimuli while the mature adults mainly used olfaction to and within the estuary but vision in the river. The homers and the subadult strayers showed a seasonal rhythm. Ecological factors that may influence the survival of the fish are discussed. The home range and migration pattern are described and analysed. Comparisons are made with other trout stocks and with the salmon stock of the Indalsälven river. Orientating mechanisms in trout homers, stayers and strayers are discussed.

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Population Estimates of Young Atlantic Salmon, *Salmo salar* L., and Brown Trout, *Salmo trutta* L., by Electrofishing in Two Small Streams in North Norway

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CONTENTS

I. INTRODUCTION

Several methods have been used to estimate fish population densities in running water. Electrofishing has become common for fish sampling during the last few decades because of the light and efficient equipment used.

In electrofishing, only part of the total number of fish whitin a sampling area is caught. The efficiency of electrofishing varies with the types of gear used, the chemical properties of the water, the physical conditions of the sampling area, the fish species and sizes, and the operators of the fishing gear (VIBERT 1967, KARLSTRÖM 1972, 1977).

To calculate the actual number of fish within a sampling area, several mathematical models have been described (RICKER 1958, MEHINICK 1963, SEBER and LE CREN 1967).

There are two main types of methods of estimating population size. These are the mark-recapture methods and the successive-removal methods.

The aim of this research is to compare these two types of methods on the same sampling areas. Both types were formerly commonly used to estimate fish population size, and are described by, among others, RICKER (1958, 1971), VINCENT (1971). In the present research, the capture-recapture estimates are based on PETERSEN's and SCHNABEL's methods (RICKER 1958, ROBSON and REGIER 1971). The removal-method estimates are based on ZIPPIN's (1958) method and regression analyses were carried out by means of the least squares method (HAYNE 1949).

The sampling area

Two small streams, Langlatbekken and Tverrelva (69° 45'N, 19° 15'E), about 20 km north of Tromsø were chosen for the experiment.

The fish fauna of the two streams consists of brown trout (*Salmo trutta* L.), atlantic salmon (*Salmo salar* L.) and eel (*Anguilla anguilla* L.). The salmon were planted as fry in both streams in 1976. Hence, the salmon populations in both streams consisted of fish of age 1+. The mean length of 1+ salmon was 6.2 cm. The trout populations in both streams consisted of fish aged from 0+ to 6+, but the estimates include fish aged from 2+ to 6+ with lengths of 8—16 cm.

The mean width of the Langlatbekken is 2 m and that of the Tverrelva 3—4 m. The mean depths of the two streams are between 10 and 30 cm and the bottom substratum is dominated by stones 10—30 cm in diameter. The water vegetation in both streams is limited, but the banks are densely vegetated, mainly by birch trees and grasses. The streams drain sloping land and the surface water velocities between the few pools that occur are between 10 and 20 cm/sec.

The sampling station in the Langlatbekken had a length of 172 m and an area of 348 m^2. In the

Tverrelva, the sampling station had a length of 345 m and an area of 1,326 m^2.

II. METHODS

The sampling stations were fenced by nets (mesh size 7 mm) during each sampling period. For practical reasons, the sampling stations were not fenced between the sampling periods. Each sampling station was electrofished three times in each sampling period, with an interval of 30 min. between each fishing run. The fish were released after each sampling period. Altogether, the sampling station in the Tverrelva was electrofished during four periods (1/7-77, 25/7-77, 24/8-77 and 15/9-77, while the sampling station in the Langlatbekken was electrofished during three periods (1/7-77, 2/8-77 and 28/8-77). The fish were marked by fin-clipping and, to check mortality due to marking, were held for at least one hour before being released.

The estimates of population size by single capture-recapture are based on the "PETERSEN method" (PETERSEN 1896) with BAILEY's (1951) modification. The variance ($\hat{V}$) of the estimate is calculated according to BAILEY (*op.cit.*).

The estimates using multiple mark-recapture are based on the SCHNABEL (1938) method. The SCHNABEL estimate is rather like a series of PETERSEN estimates, but using all accumulated data for one estimate (EVERHART *et al.* 1975). The variance is calculated according to EVERHART *et al.* (*op.cit.*).

The mark-recapture methods are fully described by ROBSON and REGIER (1971).

The estimates based on successive removals used in this research are based on ZIPPIN's (1958) method and regression analyses were carried out by means of the least squares method (HAYNE 1949). The number of individuals caught in each fishing run is plotted against the cumulative number of fish caught in the previous fishing runs. The coefficient a in the regression equation $y = -ax + b$ is a measure of the catchability.

ZIPPIN (1958) has prepared charts which simplify the use of this method. By using these charts the probability of capture during each fishing run is estimated graphically (ZIPPIN 1958). The variance is calculated according to ZIPPIN (*op.cit.*).

III. RESULTS

The results reveal large differences between the catch-recapture estimates and the removal-method estimates. There are, however, small differences within the two main methods (Tables 1—4).

The mark-recapture methods overestimate the population size when a small proportion of the population is marked. Hence the results based on mark-recapture are more reliable and give smaller confidence intervals in the last sampling period than in the previous ones.

The removal methods depend on the catch ratio between the different sampling runs and the total number of fish caught in a sampling period. The catch in previous sampling periods does not affect the results of the subsequent sampling periods. When comparing the results from these two methods, one should compare the results based on catch-recapture from the last sampling period with removal-methods estimates from the same and from previous sampling periods.

In the Tverrelva the water level was very high during the first sampling period. It is known (VIBERT 1967) that the efficiency of electrofishing decreases with increasing water level, mainly because it is difficult to see the fish owing to turbidity and high water velocity. Therefore the estimates based on the removal method for the first sampling period in Tverrelva are not directly comparable with the results obtained during the other sampling periods.

In the Tverrelva the mean estimates by the ZIPPIN regression method for the 2nd, 3rd and 4th sampling periods gave nearly 295 salmon and 145 trout. The salmon estimates varied from 232 to 373 and the trout estimates varied from 140 to 152 individuals in the different sampling periods. The PETERSEN/SCHNABEL estimates for the 4th sampling period gave 496—421 salmon and 226—219 trout. The capture-recapture method therefore gave about 68—42 % higher estimates for salmon and about 51—55 % higher estimates for trout than did the removal methods.

Table 1. *Estimated numbers of salmon in the Tverrelva.*

	1st sampling				2nd sampling				3rd sampling				4th sampling			
	n	x	N̂	CI	n	x	N̂	CI	n	x	N̂	CI	n	x	N̂	CI
PETERSEN	—	—	—	—	301	54	582	444—720	355	230	514	494—553	308	283	496	480—512
SCHNABEL	—	—	—	—	301	54	608	480—828	355	230	421	378—477	308	283	421	391—459
ZIPPIN	99	—	118	93—143	241	—	274	250—298	321	—	373	342—404	209	—	232	213—251
Regression	99	—	119	87—151	241	—	278	231—325	321	—	378	231—527	209	—	235	142—328

n =Number of fish caught in each sampling period.
x =Number of fish marked and released.
N̂ =Estimated number of fish.
CI =Confidence interval (95 %).

Table 2. *Estimated numbers of salmon in the Langlatbekken.*

	1st sampling				2nd sampling				3rd sampling			
	n	x	N̂	CI	n	x	N̂	CI	n	x	N̂	CI
PETERSEN	—	—	—	—	103	37	290	217—363	95	64	219	185—253
SCHNABEL	—	—	—	—	103	37	295	219—427	95	64	198	170—239
ZIPPIN	106	—	138	101—175	95	—	122	76—168	85	—	105	80—130
Regression	106	—	137	109—165	95	—	115	51—179	85	—	106	88—124

Table 3. *Estimated numbers of trout in the Tverrelva.*

	1st sampling				2nd sampling				3rd sampling				4th sampling			
	n	x	N̂	CI	n	x	N̂	CI	n	x	N̂	CI	n	x	N̂	CI
PETERSEN	—	—	—	—	146	73	206	173—239	156	128	215	199—231	166	150	226	215—237
SCHNABEL	—	—	—	—	146	73	208	169—270	156	128	213	187—247	166	150	219	198—244
ZIPPIN	—	—	94	86—102	134	—	140	132—148	150	—	152	148—156	138	—	141	135—147
Regression	—	—	93	87—99	134	—	141	95—187	150	—	151	147—155	138	—	141	124—158

Table 4. *Estimated numbers of trout in the Langlatbekken.*

	1st sampling				2nd sampling				3rd sampling			
	n	x	N̂	CI	n	x	N̂	CI	n	x	N̂	CI
PETERSEN	—	—	—	—	63	37	96	77—115	68	52	108	94—122
SCHNABEL	—	—	—	—	63	37	97	73—143	68	52	104	86—131
ZIPPIN	—	—	60	55—65	57	—	61	55—67	65	—	68	63—73
Regression	—	—	60	33—87	57	—	60	49—71	65	—	68	65—71

In the Langlatbekken the mean numbers estimated by removal methods in 3 sampling periods were 122 salmon and 63 trout. The estimates varied from 138 to 105 for salmon and from 60 to 68 for trout in the different sampling periods. The mark-recapture estimates for the 3rd sampling period in the Langlatbekken gave 219—198 salmon and 108—104 trout. The catch-recapture estimates for trout and salmon, respectively, were therefore 65—71 % and 62—79 % higher than the estimates based on removal methods.

IV. DISCUSSION

The validity of the mark-recapture methods depends on the following assumptions (RICKER 1958).

(a) The marked and the unmarked fish have the same mortality.
(b) The marked and the unmarked fish have the same rate of catchability.
(c) No marked fish should lose their marks, nor should any marked fish be overlooked.
(d) The marked and unmarked fish are randomly distributed.
(e) The marked fish do not migrate further than the unmarked fish and there are no additions to the population.

The assumptions of the PETERSEN method also apply to those of the SCHNABEL method, but the entire series of releases and recaptures should be conducted within a relatively short period of time so that no mortality of any kind occurs in the population (EVERHART *et al.* 1975).

The reliability of the estimations based on removal methods depends on the following assumptions (GRODZINSKI *et al.* 1966).

(a) All the individuals in the population have a uniform chance of being caught.
(b) There is either no, or very little, if any immigration and emigration of individuals during the capture period.
(c) Variation in numbers due to mortality or reproduction is slight during the capture period.
(d) Capture conditions are similar throughout the whole of the capture period.

The mark-recapture estimates in this research were carried out during a period of about two months. The natural mortality will therefore affect the estimates, especially the SCHNABEL estimates. There was a higher mortality due to marking for salmon than for trout. Because of the relatively long period between the marking and the recaptures, the marked and unmarked fish are assumed to be completely mixed. The sampling stations were fenced only during each sampling period. The fish therefore had the opportunity to move to and from the sampling stations between the sampling periods. Emigration of marked fish will cause an overestimate of the population size. The emigration of fish was examined systematically by electrofishing outside the sampling station in the Tverrelva. There was found to be very little emigration, either of salmon or of trout from the sampling area. (HESTHAGEN 1978.)

Table 5. *Estimated probability of catching salmon and trout in a fishing period.*

	Tverrelva		Langlatbekken	
	Salmon	Trout	Salmon	Trout
1st period	0.45	0.64	0.31	0.51
2nd period	0.50	0.67	0.41	0.61
3rd period	0.47	0.81	0.42	0.65
4th period	0.53	0.78	—	—

The estimates based on removal methods were made independently of previous estimates for each sampling period. Owing to the fencing of the sampling stations, premises (b) and (c) above are fulfilled for these estimates. Reduced catchability for fish that have previously been subjected to electric current has been reported by LIBORSVARSKY (1967), CHMIELEWSKI *et al.* (1973) and KARLSTRÖM (1976). Decreasing efficiency of electrofishing during successive fishing runs in a sampling period will tend to cause an underestimate of the population size within a sampling area when using removal methods. Because of previous electroshocking some fish will stay inactive in the substratum for a time and so avoid capture.

Lower catchability for salmon than for trout by electrofishing (Table 5) has been found earlier in sympatric populations (KARLSTRÖM 1972, 1977, HEGGBERGET 1977).

Because of the lower efficiency for salmon, the removal method will tend to underestimate the population size for salmon to a greater degree than for trout.

Which of the two main methods tested in this research is then to be preferred? To answer this question, one needs to know how many fish actually were in the sampling stations. The sampling station in the Tverrelva was overfished twice after the last ordinary fishing period. The station was then kept fenced for five days and again overfished. After this last fishing run, one

Table 6. *Estimation of actual numbers of fish on the sampling station in the Tverrelva caught by repeated electrofishing and treatment with rotenone.*

	Number of fish caught during ordinary sampling (3 runs)	Number of fish caught after 2 extra fishing runs	Number of fish caught 5 days later (electrofishing)	Number of fish caught by rotenone	Total
Trout	138	8	16	5	167
Salmon	209	62	26	55	352

Table 7. *Cumulative numbers of fish marked in the sampling periods.*

	Sampling periods 2	3	4	Unmarked fish caught during the last sampling period	Total number of fish
Trout, Tverrelva	104	178	202	18	220
Trout, Langlatbekken	57	83	99	9	108
Salmon, Tverrelva	109	356	481	25	506
Salmon, Langlatbekken	106	172	236	4	240

fifth (the lower part) of the sampling station was treated with rotenone.

The numbers shown in Table 6 represent a minimum of fish in the last sampling period. Because of low water temperature, both electrofishing (Vibert 1967) and rotenone (Gesdorf 1943) have a low efficiencey. Table 6 therefore indicates an underestimation of fish by the removal methods (Tables 1 and 3).

Another way of calculating the total amount of fish would be to sum the total numbers of fish marked in all sampling periods at each sampling station and add this to the numbers of unmarked fish caught in the last sampling period.

The fish that were killed owing to marking are also included in Table 7. The numbers of fish in this table include all the fish marked in the period from the beginning of July to the beginning of September. Because of possible migration between the sampling periods, these numbers are not exact, but they are thought to be a good indication of the real numbers of fish at the sampling station. When comparing Tables 1 and 7, it will be seen that in order to get a reliable estimate using the mark-recapture method, from one half to three quarters of the population has to be marked. Analysis of migration in the Tverrelva during this period showed that 16 salmon and 10 trout emigrated from the sampling station, while 6 trout immigrated into the sampling station from the upper parts of the stream (Hesthagen 1978).

The calculated total number of fish (Table 7) fits well with the estimates based on mark-recapture. For salmon, the estimates based on the Petersen method are in accordance with the numbers in Table 7, while the estimates based on the Schnabel method are lower.

This indicates that the catch-recapture methods give the best results, while the estimates based on removal methods underestimate the population size by about 50 %. The fact that 90—95 % of the individuals were marked in this experiment is also an indication of the reliability of the mark-recapture estimates. The main reason for the underestimation of the population size by the removal method is the reduced catchability of fish that have already experienced electric current earlier. In a small stream, all fish within the fenced area will be affected by the electric current during each fishing run. After the first fishing run, some of the fish that were not caught will hide among stones and vegetation and stay there inactive for a shorter or longer period.

Other authors who have made comparisons between these two main methods have also found differences. Timmermans (1957) found that mark-recapture gave higher estimates than did removal methods. Karlström (1976) analysed the two methods and found that the successive-removal method gave fairly good significance levels for the population estimates of young salmon and trout, even at low population size. Karlström (*op. cit.*) also mentions that the emigration of marked fish and inconsistent mixing of marked and unmarked fish can make the mark-recapture estimates unreliable. Herbert *et al.* (1961) concluded that both methods gave good estimations of population sizes, while Elson (1967) obtained more precise population estimates with Schnabel's method than with the removal method.

V. SUMMARY

Mark-recapture and successive-removal methods using electrofishing were analysed at the same sampling stations in two small streams near Tromsø, northern Norway. The mark-recapture estimates were carried out by using the Petersen and Schnabel methods, while the removal-method estimates were obtained by Zippin's method and regression analyses, performed by means of the least squares. The results showed that the catch-recapture method gave fairly good estimates, while the removal methods underestimated the population size by about 50 %. One of the main reasons for the underestimation by removal methods in fenced areas in small rivers is thought to be the reduced catchability of fish that have already previously have experienced electric current. Because of lower efficiency for salmon, the removal methods tended to underestimate the population size to a greater degree than for trout.

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Growth and Yield of an Alpine Population of Brown Trout, *Salmo trutta* L., in Eastern Norway

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CONTENTS

I. INTRODUCTION

Lake Sylvetjern is located in eastern Norway at an altitude of 1,401 m and is well known for its population of large brown trout. It was therefore of special interest to initiate a study of the growing conditions and estimated annual yield in order to determine the reason for this lake's productiveness.

The lake was stocked with fry for the first time in 1935; six years later it was fished with nets. Seven fish were then taken, with a total weight of 28 kg. During the following years the people who leased the lake took large catches. In 1953, 450 trout were netted during three nights, producing a total weight of about 450 kg and a yield of more than 10 kg/ha. The largest fish ever caught weighed 10 kg. Lake Sylvetjern was privately leased until 1963; since that time it has become a popular fishing spot among the local people. Generally the fish are caught with the use of the otter. Gill-netting has not been allowed.

Studies pertaining to alpine populations of brown trout are scarce. SØMME (1934), in his work on the brown trout of Hardangervidda (altitude approximately 1,200 m) in western Norway, stated that fish lengths of 50—60 cm and ages of 13—14 years were common. Yields of 0.2 and 0.5 kg/ha for two lakes were reported. Large variations from year to year were, however, noted. JENSEN (1959), in his study dealing with three small lakes in the same area, reports average yields during fifteen successive years of 2.7, 3.3 and 3.6 kg/ha.

Trout populations in Lake Øvre Heimdalsvatn (altitude 1,090 m) have been more thoroughly studied. The average yield during the years 1958—70 was 5.2 kg/ha (JENSEN 1974). During three successive years of study on Lake Langtjern (altitude 1,030 m) SVENDSEN (1962) calculated an average yield of 9.3 kg/ha.

II. METHODS AND MATERIALS

Monofilament gill nets with knot-mesh sizes of 22, 24, 26, 29, 32, 35 and 39 mm were used during the study periods of 1970 and 1975.

All captures in 1976 were taken by using otter. The fish length is defined as total length. The scale samples were taken in the area between the front of the adipose and the back of the dorsal fin (DANNEVIG and HØST 1931). Impressions of scales were on celluloid, examined and measured by using a scale projector.

The exponent b in the general length-weight equation $W = a\ L^b$ was calculated by using log transformation by means of the least squares method. According to this method, $b=2.963$ and the confidence interval is 2.88—3.04 ($p=0.95$). Thus, to determine the coefficient of condition the formula $W=a\ l^3$ (*i.e.* isometric growth) is used.

Transformation of log fish length (y) — log scale length (x) gave the expression $y=0.21+0.94 \cdot x$ ($r=0.73$). The regression coefficient b_{xy} is close to 1.00, hence the growth of fish and scale is isometric. A direct proportion between these two parameters is accepted and DAHL's (1910) method can be applied.

VON BERTALANFFY's growth equation,

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

is used to express the condition of growth of this brown trout populations. L_∞, the value of l for which the rate of growth is zero, is estimated according to WALFORD (1946) by means of the least squares method for $l_t \geq 3$. K, a measure of the rate at which length approaches L_∞, can be estimated from the slope of the regression line, which is $e^{-Kt} \cdot t_0$, the theoretical age at which $l=0$, is calculated according to GULLAND (1973).

The yield estimated for 1976 was established mainly by giving anglers scale envelopes, by interviewing, and by personal field work. The fish in the biomass estimates were weighed and divided into 50 g intervals and average values in each interval were used.

The total sample for back calculation consists of 91 specimens, taken as follows. In 1970 the sample was 18 fish, from which scales were removed and studied. The total yield for 1975 was 74 and scale samples from 18 were utilized. The total yield during 1976 was 268 trout. Of these, 70 were sampled for weight and length, and scales were taken from 55 specimens.

III. DESCRIPTION OF THE STUDY AREA AND ITS BIOLOGICAL CAPACITIES

Lake Sylvetjern is situated in Lom municipality, Oppland County, at 61° 45'N, 8° 49'E. The lake has an area of 0.44 km^2: total watershed is 4.0 km^2 with an alkaline bedrock. The flora in the vicinity is sparse: *Salix spp.* and *Betula nana* grow among bare rock, scree and barren ridges. The shoreline consists mostly of stone.

The lake, which is oligotrophic, has a mean depth of 10.5 m. The water is poor in nutrients with 3 mg "CaO"/l., and the pH averages 6.6.

Natural reproduction of the trout is not thought to occur. Spawning facilities in the outlet are very limited; the inlet flows through scree, eliminating spawning facilities. In alternate years, therefore, the lake is stocked with 400—500 fingerlings.

The main trout food available consists of *Lepidurus arcticus* and *Gammarus lacustris*, as indicated by stomach samples (*cf.* HESTHAGEN 1979, SEGERSTRÅLE 1954). However, the latter species has not been observed in recent years. Stomach samples frequently contained Chironomidae. Also of importance as fish food are *Lymnea spp.* Fish remnants were not found in any of the stomachs examined.

IV. RESULTS

Growth

The growth pattern of the brown trout population in Lake Sylvetjern, though even in the second, third and fourth years declines thereafter without any sign of stagnation (Table 1). Accordingly, the growth cycle may be divided into four groups:

1. A relatively modest growth rate in the first year, with a length averaging 43 mm.
2. A rapid growth rate in 2nd, 3rd and 4th years with yearly average growth of 66 mm.
3. A somewhat slower rate from the 5th to the 7th year, averaging 49 mm.
4. A more pronounced reduction in growth rate after 8 years.

The weight-length equation is expressed by $W=0.0014 \cdot l^{2.963}$ ($r=0.989$). Fig. 1 shows the Walford plot between l_t and l_{t+1} expressed by the formula $y=0.862 \cdot x+9.03$ ($r=0.998$). L_∞ was further estimated at 64.5 cm, $K=0.15$ and $t_0=0.82$.

The population's growth equation is now defined by

$$l_t=64.5\ (-e^{-0.15\ (t-0.82)}).$$

Table 1. *Back-calculated growth length at age t(l^t).*

	l_1	l_2	l_3	l_4	l_5	l_6	l_7	l_8	l_9	l_{10}
Calculated length	43	106	171	240	292	341	388	426	460	483
Yearly growth increment	43	63	65	69	52	49	47	38	34	23
No of fish examined for l_t	91	91	88	80	57	13	12	8	6	3

The growth pattern is also consistent with the Walford plot. The oldest fish from Sylvetjern was 17 years old and 64 cm long (Fig. 2). Two fish 13 years old were also reported.

Condition factor

The average condition factor of the 1975 sample for each length interval of 1 cm is shown in Table 2. Generally speaking, such condition factors for the stock are considered good, with values ≥ 0.97. An increase seems to have taken place for bigger fish, *e.g.* for those ≥ 26 cm.

Length distribution from otter- and gill-net catches

When these two length distributions are compared, an obvious difference emerges (Fig. 3).

A modest distribution is noted for the fish taken by gill nets, with lengths in the neighbourhood of 23—31 cm dominating (averaged 26.8 cm). These are predominantly four-year-old fish.

The fish caught by the otter range over a greater length interval and consequently this method harvests most of the year classes in the fish population. Fish caught on this gear averaged

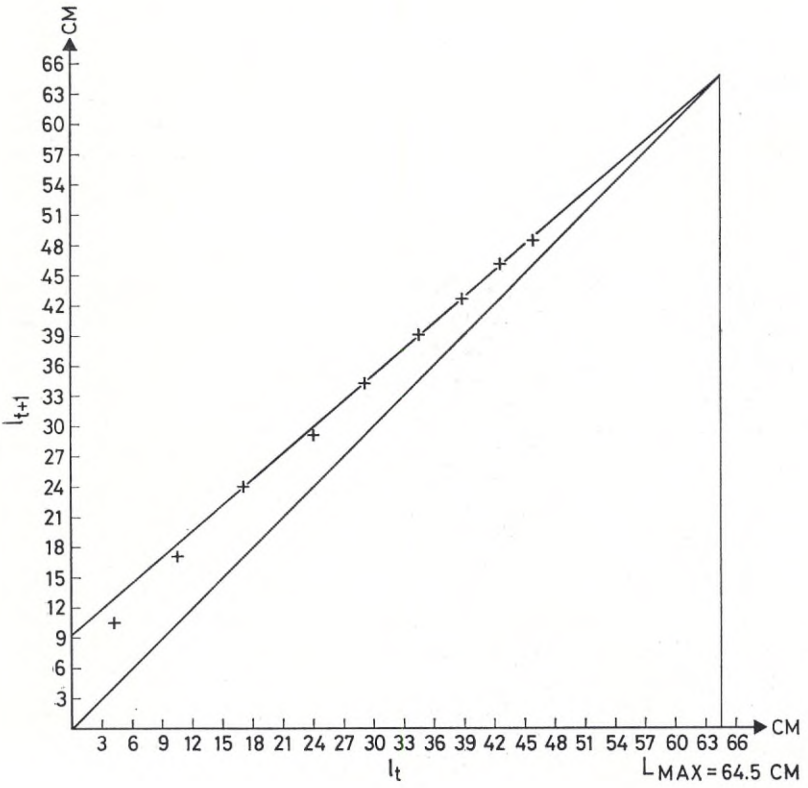

Fig. 1. Estimation of L_∞.

Table 2. *Mean condition factor at length interval.*

Fish length (cm)	21	22	23	24	25	26	27	28	29	30	31	32	33
Condition factor ($\bar{x}$)	0.99	1.00	0.97	0.97	1.00	1.05	1.06	1.06	1.09	1.05	1.08	1.04	1.08
Standard deviation	0.03	0.07	0.08	0.09	0.06	0.07	0.11	0.05	0.03	0.02	0.07	0.03	0.08
No of fish	4	3	6	3	13	6	10	9	5	4	5	3	2

34.1 cm in length. Besides giving a high yield, ottering is a good form of sport fishing and it enables the angler to catch the larger fish. These larger (and older) fish indicate a relatively low fishing mortality in the population.

Yield

The estimated total catch was determined at 162.6 kg (Table 3). This quantity is distributed almost equally above and below the 625-g level. Fish in the interval 400—500 g contributed most to the estimated yield. The sample of 162.6 kg in 1976 produces a yield of 3.7 kg/ha.

It is assumed that the distribution of the total catch would correspond closely to that of the 70 fish with known weights.

V. DISCUSSION

It is thought that a large percentage of the catch in 1976 was recorded. The author was the district game warden and the most avid fishermen were local people. However, the estimated yield is a minimum. In the author's experience, the fishing effort and documented yield in Lake Sylvetjern in 1976 represent an average year. Thus the estimated yield of 3.7 kg/ha should give a good indication of the annual yield.

Fish production compared with yield is unknown in Lake Sylvetjern. In Lake Øvre Heimdalsvatn, JENSEN (1974) estimated that the yield was only about 25 % of the fish production in 1970. The average yield in this lake has been 5.2 kg/ha between 1958—70 (JENSEN *op.cit.*), and the annual exploitation rate about 45 % (JENSEN 1970).

The length distribution of the otter catch indicated a high proportion of older fish in the population, a fact which suggests low fishing mortality. Theoretically, production could have accumulated over some years, and a high fishing intensity in 1976 could have caused a higher yield than the production that year.

The length distribution from the otter catch (low fishing mortality) indicates that production and hence, the yield could possibly have been higher with a faster turnover rate for the population. To accomplish this, harvesting by gill nets will have to be considered. With the special form

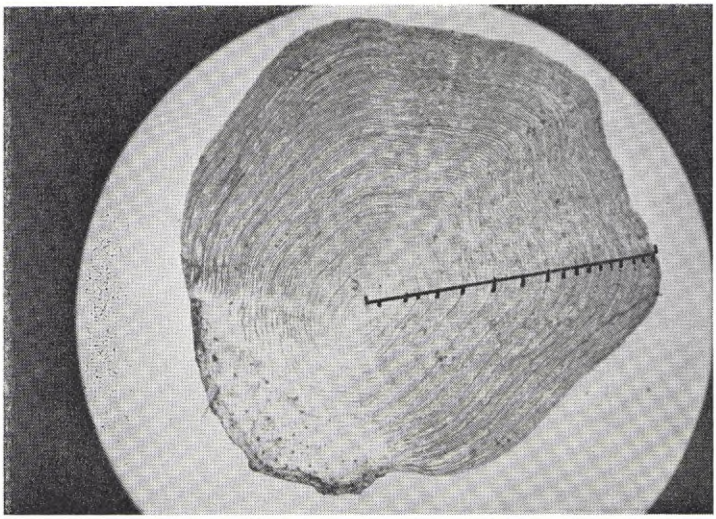

Fig. 2. Scale of the 17-year-old fish caught in 1976, which was 64 cm long.

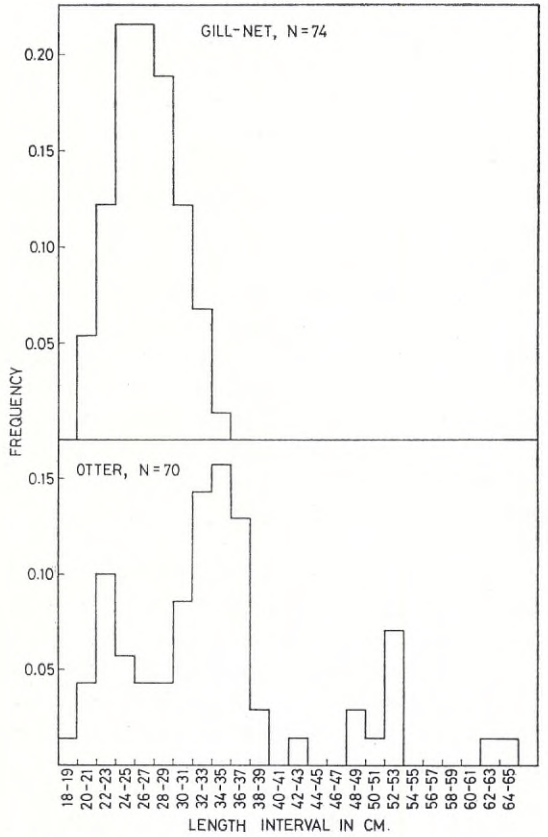

Fig. 3. Length distribution from otter- and gill-net catches.

of harvesting which prevails in Lake Sylvetjern today, and with the present stocking intensity, a sustained yield of about 4 kg/ha annually seems reasonable. This figure could probably be exceeded without overexploiting the stock. However, the relation between density (*i.e.* stocking intensity) and growth, combined with different fishing intensity, is unknown for this brown trout population.

In evaluating the high yield in Lake Langtjern reported by SVENDSEN (1962), one must take into consideration that the lake was privately owned. This made controlled fishing (gill-netting) possible and the stock was exploited at a rate of about 50 % annually.

SØMME (1934) mentioned overexploitation as a possible cause of low yield in different lakes on Hardangervidda. The recruitment age of these harvested stocks was as low as 3—4 years, and the fishing on older year classes was very intense.

When the growth rate of the population in Lake Sylvetjern is compared with that of different populations of brown trout in high mountain lakes reported by OLSTAD (1925), SØMME (1934) and SVENDSEN (1962), it is found that the growth rate in Sylvetjern is relatively slow in the first four years, but thereafter improves and is even better for older fish. The growing condition in Lake Sylvetjern is distinctive in that it decreases evenly throughout the entire life cycle. The fish commonly attain lengths of 50—60 cm, which is in good agreement with SØMME (1934), whose studies included the trout populations of Hardangervidda.

VON BERTALANFFY's growth equation is used to express the growth pattern of this population. However, a shortcoming of this method is the great variation, found by JENSEN (1977), in the equation's parameters between different years. But, as stated, the result in this paper represents an average from samples taken in three different years.

The large fish described are the result of a continued growth into old age. This is thought to be achieved on an invertebrate diet, as no fish were found in the stomachs examined. A better condition factor for bigger fish can be a reflection of a partial change in diet. Fish smaller than about 27 cm had fewer *Lepidurus arcticus* in their stomachs, compared to bigger fish.

In spite of the fact that Lake Sylvetjern is situated at an altitude of 1,401 m, the brown trout population which inhabits the lake demonstrates a surprisingly high growth rate and seems capable of sustaining a high yield.

VI. SUMMARY

The growing condition of a population of brown trout (*Salmo trutta*) was studied and yield was estimated for one year in the alpine Lake Sylvetjern, situated in eastern Norway at an altitude of 1,401 m.

The length-weight relationship fits the function

$$W=0.014 \cdot l^{2.963} \ (r=0.989).$$

By using VON BERTALANFFY's growth equation, the growth pattern is defined:

$$l_t=64.5\ (1-e^{-0.15\ (t-0.82)}).$$

Table 3. *Estimated total yield distributed in weight intervals.*

Weight interval (g)	Mean weight	No of fish in interval	Multiplier	Estimated biomass in interval (kg)
50— 99	75	1	3.83	0.29
100— 149	125	10	38.30	4.79
150— 199	175	2	7.66	1.34
200— 249	225	5	19.15	4.31
250— 299	275	2	7.66	2.11
300— 349	325	5	19.15	6.22
350— 399	375	2	7.66	2.87
400— 449	425	11	42.13	17.91
450— 499	475	9	34.47	16.37
500— 549	525	6	22.98	12.06
550— 599	575	1	3.83	2.20
600— 649	625	4	15.32	9.58
650— 699	675	—	—	—
700— 749	725	1	3.83	2.78
750— 799	775	—	—	—
800— 849	825	1	3.83	3.16
1300—1349	1325	1	3.83	5.07
1500—1549	1525	1	3.83	5.84
1600—1649	1625	1	3.83	6.22
1700—1749	1725	2	7.66	13.21
1750—1799	1775	2	7.66	13.60
2200—2249	2225	1	3.83	8.52
2750—2799	2775	1	3.83	10.63
3500—3549	3525	1	3.83	13.50
Total yield				162.6

The growth pattern decreased evenly throughout the life cycle. The growth rate was, however, highest between the second and fourth years, averaging 66 mm. No growth stagnation was observed.

A higher condition factor emerged for larger fish and is thought to be a result of a change in diet. The growth appears to be attained through an exclusively invertebrate diet.

A significant difference in length distribution between otter catches and those from gill nets — was discovered.

In 1976 a yield of 3.7 kg/ha was estimated, which is thought to represent an average year.

VII. ACKNOWLEDGMENTS

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On the Use of a Stochastic Model for Simulating Yields from a Trout Lake

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CONTENTS

I. INTRODUCTION

In a previous paper (JENSEN 1977) a deterministic yield model was used for computer simulations of the gill net fishery in a Norwegian trout lake. Among the variables in the model were temperature, number of recruits and mean weight of recruits. In order to simplify the simulations mean values were used for these variables. In this article consequences of treating temperature and recruitment as stochastic variables are examined.

II. MATERIALS AND METHODS

The temperature variable (T_6) is as before the mean June air temperature at Vågåmo. The 27 observations covering the years 1949—75 were used. The range of these means was 10.3°C—15.9°C, their mean 12.185°C and the standard deviation of the sample 1.5649°C. As a rankit plot showed considerable deviations from a straight line, a normal distribution of the temperature means was not accepted, but we used a computer program giving each of the observed 27 values equal probability of entering each year's simulation.

For the recruitment we have estimates of the numbers (range 2127—5698) and mean weights range 34.3—41.6 g) of four-year old fish on 1 June in 12 years. Tentative plots of numbers of recruits on approximate egg numbers in the parent generations gave so slight indications of association between these variables that it was not attempted to construct a recruitment curve. This was not unexpected for a material of only 12 sets of observations and probably a very high error variance. Neither was any significant correlation found between the number and mean weight of the recruits. Recruit number and mean weight were therefore treated as stochastic variables that were independent of each other. Again the computer program generated for each year an equal probability of being represented for each of the 12 weight values and for each of the 12 values for numbers of recruits.

For the stochastic model we simulated 400 years' fishing with yearly effort 800 gill-net nights.

In one alternative the effort was divided equally on nets with mesh sizes (knot to nearest knot) 24 mm and 36 mm. In another 400 years' run the mesh sizes were 26 and 32 mm.

For the deterministic model was for each year used mean number (3539) four-years trout with mean weight 38.2 g and the mean temperature 12.185°C. The fishing effort and the mesh sizes were the same as in the stochastic model.

For both models the starting point for the simulation runs were the estimated numbers and mean weights of trout in Lake Ø. Heimdalsvatn 1 June 1960 (see table 33 in JENSEN 1977).

In statistics SOKAL and ROHLF (1969) has been used.

Table 1. *Ø. H. Sustained fishing with 24 and 36 mm nets. Effort 800 net-nights/year.*

Deterministic model: Yield: 280 kg. Density 14.6 kg/ha.

Stochastic model:

Period	Yield $\bar{Y}$	Range for Y	s_Y	Density $\bar{D}$	Range for D	s_D
1	273.3	225—372	32.65	14.5	11.2—17.2	1.38
2	279.6	211—360	36.95	14.9	10.9—19.4	1.90
3	262.7	214—350	33.66	13.8	11.3—17.6	1.36
4	269.2	203—365	40.80	14.5	11.5—19.1	2.10
5	286.9	214—363	32.75	15.3	12.0—18.9	1.40
6	275.2	216—339	31.23	14.8	12.1—17.9	1.29
7	283.5	212—356	34.49	15.2	11.6—18.0	1.70
8	277.8	224—373	32.90	14.8	11.9—18.1	1.49

$\bar{\bar{Y}}=276.03$ $s_{\bar{Y}}=7.767$ $\bar{\bar{D}}=14.73$ $s_{\bar{D}}=0.474$

III. RESULTS

The results of the simulations for the two mesh combinations are shown in Tables 1 and 2. The 400 years' stochastic simulations have been divided in 50-years periods. The deterministic simulations gave equilibrium yields after only 10—15 years and these Y_E-values are listed in the tables.

For yearly effort 800 net-nights with meshes 24 and 36 mm the deterministic model predicted an equilibrium yield of 280 kg. The corresponding stochastic model gave for 400 years a mean yield of 276 kg. The standard error of this mean was only 7.8 kg. The yearly variation in yield was considerable and ranges from 211 to 373 kg. The eight 50-years yield means had a range of 263—287 kg with coefficients of variation (sample standard deviation as percentage of sample mean) varying between 11.4 and 15.2.

The population density on 1 June predicted by the deterministic model was 14.6 kg/ha while the stochastic model gave a 400-years mean of 14.7 kg/ha. Also for this variable the yearly variation was considerable with range 10.9—19.4 kg/ha and coefficient of variation ranging from 8.7 to 14.5 in the eight 50-years periods.

For yearly effort 800 net-nights with 26 and 32 mm nets the deterministic model predicted an equilibrium yield of 296 kg, while the stochastic model predicted a 400-years mean of 295 kg. The coefficient of variation had a range of 11.9—17.1 for the eight 50-years periods. The population density predicted by the deterministic model was 14.4 kg/ha, and the mean value predicted by the stochastic model was also 14.4 kg/ha. The coefficient of variation for 50-years periods had a range of 8.6—15.7.

The two distributions of 400 yields generated by the stochastic model were slightly skewed to the right. For the 24—36 mm nets the distribution was not significantly different from the normal distribution, for the 26—32 mm nets the difference was significant. Apparently predictions of probable yields would not be substantially biassed by treating the yields as normal deviates with the means and standard deviations generated by the model. If more stochastic variables were included in the model, this trend towards normality would probably increase.

IV. DISCUSSION

The lack of a proper recruitment model excludes predictions of recruitment overfishing and eventual collapse of the fishery. According to the model the yearly recruitment could not come below 2127 4-years trout even if not a single egg had been produced by the parent generation.

Table 2. *Ø. H. Sustained fishing with 26 and 32 mm nets. Effort 800 net-nights/year.*

Deterministic model: Yield 296 kg. Density 14.4 kg/ha.

Stochastic model:

Period	Yield $\bar{Y}$	Range for Y	s_Y	Density $\bar{D}$	Range for D	s_D
1	294.9	226—416	42.87	14.0	10.8—16.4	1.21
2	296.3	215—432	47.65	14.5	10.6—19.0	1.94
3	274.1	202—377	39.76	13.6	11.2—16.6	1.37
4	288.5	203—409	49.43	14.1	10.9—19.0	2.21
5	307.0	215—439	45.07	14.8	11.6—18.7	1.48
6	295.8	216—367	35.30	14.5	11.7—17.0	1.37
7	303.3	214—394	45.49	14.9	11.1—17.9	1.72
8	296.6	216—418	44.54	14.4	11.4—17.4	1.46

$\bar{\bar{Y}}=294.56$ $s_{\bar{Y}}=9.967$ $\bar{\bar{D}}=14.35$ $s_{\bar{D}}=0.431$

However, if the fishery in this lake is not concentrated on the spawners (closing in- and outlet with net or traps, net fishing on spawning places etc.) recruitment overfishing is very unlikely. During the investigations the biomass of spawning female trout varied in the proportion 1: 8 or 1: 10 while the variation in the number of 4-years recruits was only 1: 2.7. A high proportion of the early mortality is therefore probably density dependent. This will tend to reduce the variation in recruitment and reduce the probability of recruitment overfishing.

Beverton and Holt (1957, p. 22) stated: "It is our belief, however, that except in particular instances which have been indicated in the text (*e.g.* in § 6, dealing with the egg — recruit relationship), the multiplication of effort both in deriving the stochastic equations and in computing them would not have been justified when the standard of accuracy of our data, the complexity of the biotic system with which we are dealing, and the order of magnitude of the expected discrepancies, are all taken into account".

Leslie's (1958) results may also give the impression that for stocks above a certain size it is hardly worth while to complicate the models by introducing probabilistic variables. However, on the modern computers the extra work and costs by using stochastic modelling need not be overwhelming, and the simulated variations in yield are more realistic and can be more useful and informative than the nonexistant equilibrium state. The recent collapses of some important marine fish stocks may also emphasize the need of stochastic simulation of the stock-recruitment relationship and, as a later step, dynamic programming in the sense of Walters (1975) of important fisheries.

V. SUMMARY

Temperature and recruitment were handled as stochastic variables in simulations of yield from a trout lake. In the chosen model recruitment was independent of the size of the parent stock and a collapse of the stock impossible. The yearly variation in simulated yields at constant fishing effort was substantial, but the means for 50-year sequences were very near the equilibrium yields predicted by the corresponding deterministic models.

VI. ACKNOWLEDGMENT

I am indebted to professor Øyvind Nissen of the Computer Center of the Agricultural College of Norway, who took care of the programming and gave valuable advise.

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Demographic Strategy in Char Compared with Brown Trout in Lake Løne, Western Norway[1]

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CONTENTS

I. INTRODUCTION

The aim of the present paper is to compare the demographic strategy of char (*Salvelinus alpinus* (L.)) with that of brown trout (*Salmo trutta* L.) in Lake Løne, Western Norway. The demography of the brown trout population has been discussed by JONSSON (1977).

In Lake Løne, the population of brown trout is highly superior in number compared with the char; this is in contrast to what is found in most other localities studied (HUITFELDT-KAAS 1918, SØMME 1941, FILIPSSON and SVÄRDSON 1976). The char and the brown trout population in Lake Løne are landlocked. Three kilometres below the lake, the river forms a waterfall, Rognsfossen, which isolates these stocks from the populations found downstream. Besides char and brown trout, Lake Løne supports a landlocked population of three-spined stickleback (*Gasterosteus aculeatus* L.), and catadromous eel (*Anguilla anguilla* L.). The study area and fish populations are further described by MATZOW *et al.* (1976), and JONSSON (1977).

II. MATERIAL AND METHODS

During the period June 1972—September 1973, 944 char were collected in Lake Løne, Western Norway. The monthly catches are given in Table 1. In order to catch char representing the various length groups found in the population (JENSEN 1973), both bottom and floated nets (mesh-sizes 5—45 mm) were used. A detailed description of the sampling techniques used is given in JONSSON and MATZOW (1979, ch. 11). The net catches consisted mainly of fish longer than 15 cm, although specimens as small as 10 cm were captured. The material and sampling methods for trout are given in JONSSON (1977).

The fish were measured to the nearest 0.5 cm from the tip of the snout to the outer lobes of the tail as the fish lay naturally distended. This resulted in a maximum error of 2.5 %.

The sex and degree of sexual maturity were determined as described for trout by DAHL (1917, p. 36—37). Applying this system, it was possible to distinguish between sexually immature and mature specimens in the period August—January.

For char, individual fecundity (*sensu* NIKOLSKY 1969, p. 32) was investigated by counting the total number of ripe eggs in the ovaries of a random sample of 12 females in maturity stage

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Table 1. *Monthly catches of char, Salvelinus alpinus (L.), in Lake Løne, Western Norway.*

Year	Month	No of char
1972	June	25
”	July	180
”	August	99
”	September	120
”	October	194
”	November	13
1973	January	55
”	April	102
”	May	64
”	June	75
”	September	17
Total		944

IV (*cf.* Dahl 1917, p. 36) with body lengths between 26—29.5 cm.

The age of the char was determined by use of the otoliths (Nordeng 1961, Østli 1976), prepared and treated as for brown trout (Jonsson 1976). It was found that otoliths from 914 char (96.8 % of the total material) were suitable for age determination. The age groups were designated as recommended by the I.C.N.A.F. (Jensen 1965).

As for brown trout (Jonsson 1977), measurements of the outer opaque otolith zones of char were used as a relative index of the fish growth. The correlation coefficient (Snedecor and Cochran 1967) between the otolith radius (r_1) (*cf.* Jonsson and Stenseth 1977) and the fish length was estimated equal to 0.89. The otoliths were measured to the nearest 0.01 mm, the error due to measurment (Jonsson and Stenseth 1976) being estimated equal to 0.02 mm.

All statistical tests in the present paper are based on a 5 % significance level.

III. RESULTS

Age and sex distribution

The age distribution of char caught is given in Fig. 1.

In age group 1, only a few fish were caught. Age groups 2—5 account for about 94 % of the total catch. Individuals older than 5 years are few. Natural mortality and fishing activities account for the decline in number.

The age at which sexual maturity is reached is shown in Table 2. The Løna char (char in Lake Løne) mature sexually fairly synchronously, most of them in age group 4, though first-time spawners are also observed in age groups 3 and 5. The brown trout in Lake Løne show much more heterogeneous age at sexual maturation. According to Jonsson (1975, 1977), male trout mature in age groups 2—7, the females in age groups 3—7. More recently, mature males in age group 1 have also been observed in Lake Løne (Jonsson unpubl.).

The sex distribution is given in Table 3. In the two youngest age groups, there is a predominance of males in the catches; in age groups 3—4, the sex ratio is close to 1. Among older char, there is a significant excess of females in the catches tested as recommended by Snedecor and Cochran (1967, p. 211—213)). Males and females reach sexual maturity at about the same age. The dominance of females in the oldest age groups thus appears not to be connected with the age at which sexual maturation occurs as found for brown trout (Jonsson 1977).

Alm (1959) maintained that males in many species are more active than females, and are thus more heavily exposed to predators and fishing gear. The predominance of males in the catches of the two youngest age groups may indicate that such factors are responsible for the dominance of females in the oldest age groups, though this cannot be verified with certainty in the present material.

The year-class frequencies in the catches taken during the period September 1972—June 1973 are shown in Fig. 2.

The catch of year class 1970 may be expected to be somewhat underrepresented because these fish are less catchable than older ones owing to smaller body size. For char, the figure indicates that every third year (*viz.* 1964, 1967, 1970) gives rise to a rather strong age group. The same tendency was indicated by catches taken during the autumn of 1976, where the year class 1970 and 1973 appeared to be rather strong (unpubl. data). For brown trout, no year-class fluctuation has been found. In Lake Løne, the trout may thus have a more stable recruitment than the char.

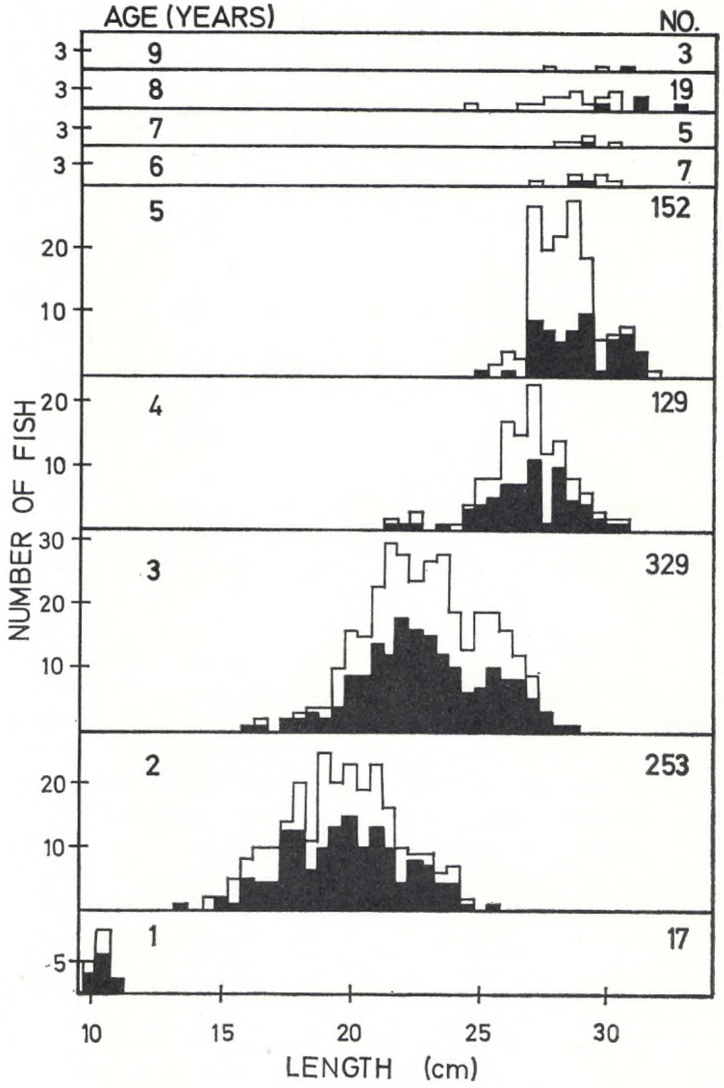

Fig. 1. Age distribution of char, *Salvelinus alpinus* (L.), caught from June 1972—September 1973 in Lake Løne, Western Norway.

■ = males, □ = females.

Table 2. *Sexually immature and mature char, Salvelinus alpinus (L.), caught from August 1972—January 1973 in Lake Løne, Western Norway.*

	Males		Females		
Age	Immature	Mature	Immature	Mature	Total
1	11	—	6	—	17
2	96	—	74	—	170
3	58	7	45	2	112
4	11	15	3	27	56
5	1	40	—	63	104
6—9	—	5	—	16	21
Total	177	67	128	108	480

Table 3. *Distribution of male and female char, Salvelinus alpinus (L.), caught from June 1972—September 1973 in Lake Løne, Western Norway.*

Age	Males	Females	Total
1	11	6	17
2	147	106	253
3	176	153	329
4	63	66	129
5	58	94	152
6—9	8	26	34
Total	463	451	914

Growth rate and fish length

As a relative index of the monthly growth rate of the char, measurements of the width of the outer opaque growth zone of the otoliths in age groups 2—5 are given in Fig. 3 (*cf.* Jonsson 1977). The figure shows that the char grow rapidly from June to September. Later in the autumn, fish growth appears to be rather slow, or even non-existent. A similar growth pattern was observed for brown trout (Jonsson 1977). In age group 4, the opaque zones of the otoliths of sexually immature char are somewhat wider than the corresponding zones in the otoliths of mature specimens at the end of the growth season. According to Student's 't' test, however, this difference is not significant. Thus, in this population of char, the zone width of the otoliths cannot be used with certainty to determine the age of sexual maturation as, *e.g.*, Nordeng (1961) found for char in the Salangen river system, Northern Norway.

The average lengths of the char in age groups 2—5, caught from September 1972—January 1973 (when most of the char had ceased to grow), are given in Table 4. As can be observed, there is no significant difference in size between sexually immature and mature males or females within any age group.

The fish length when sexual maturation is reached is much more homogeneous for char than for brown trout in Lake Løne (*cf.* Jonsson 1977). The shortest mature male char observed was 22 cm, the shortest female 24 cm. The corresponding lengths for brown trout were 10.5 cm and 19.5 cm, respectively.

The length-frequency distribution for age groups 2—5 (year classes 1967—70) of char and brown trout caught during the period September 1972—January 1973 is given in Fig. 4. The char grow on average somewhat faster than the trout. However, both species normally grow to a maximum body length of 30—35 cm in Lake Løne. It can be observed that the char are more homogeneous in length than the trout in all age groups examined, and that the difference is most pronounced in the oldest age groups.

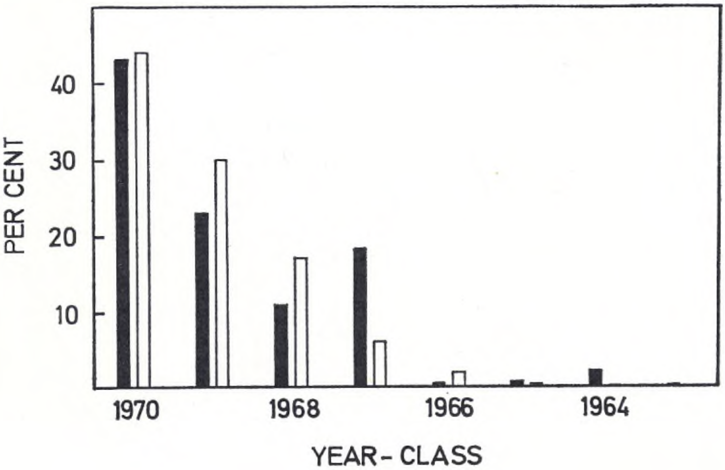

Fig. 2. The percentage year-class distribution of char, *Salvelinus alpinus* (L.), and brown trout, *Salmo trutta* L., caught from September 1972—June 1973 in Lake Løne, Western Norway.

■=char, □=brown trout

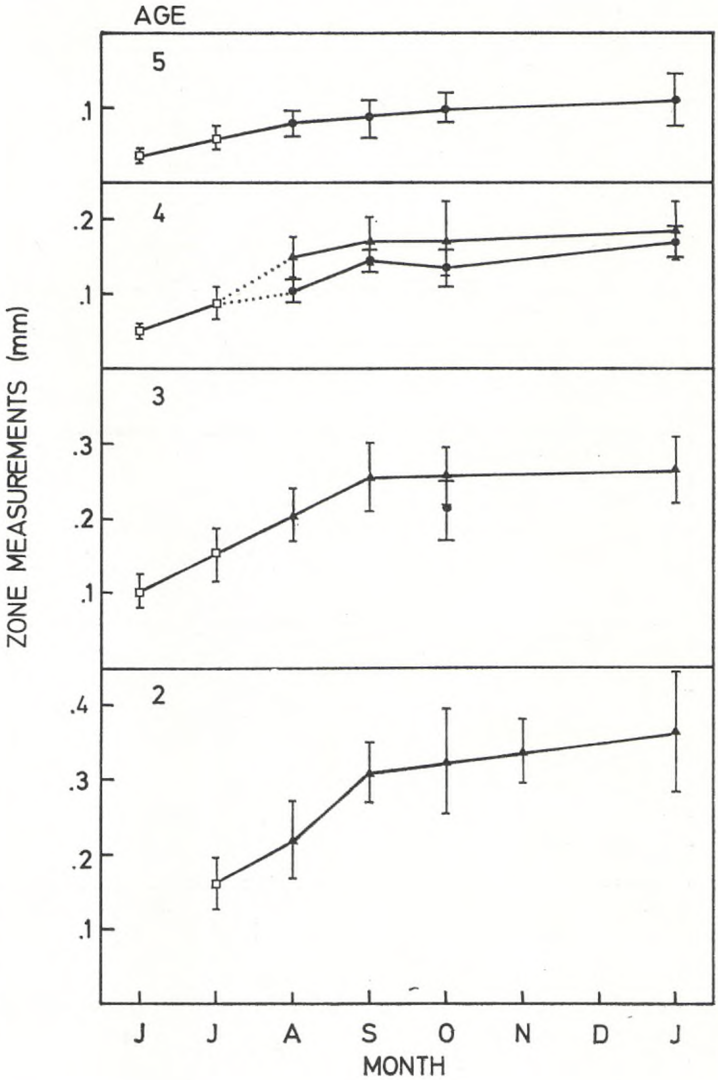

Fig. 3. Width of the outermost opaque otolith zone with 95 % confidence limits of the measurements. Char, *Salvelinus alpinus* (L.), caught from June 1972—January 1973 in Lake Løne, Western Norway. Dotted line indicate the connection between the measurements in months when the material is divided into sexually immature (▲) and mature (●) individuals, and months when these two categories are not separated (☐).

Table 4. *Average length (cm) of sexually immature and mature char, Salvelinus alpinus (L.), caught from September 1972—January 1973 in Lake Løne, Western Norway (C. l.=95 % confidence limits).*

	Males				Females			
	Immature		Mature		Immature		Mature	
Age	Length	C.l.	Length	C.l.	Length	C.l.	Length	C.l.
2	20.0	0.4	—	—	19.7	0.5	—	—
3	24.5	0.6	23.6	1.8	24.3	0.6	25.0	—
4	27.1	1.0	27.2	0.9	29.5	—	27.2	0.5
5	—	—	28.7	0.4	29.0	—	29.1	0.3
6—9	—	—	30.2	2.2	—	—	28.5	1.0

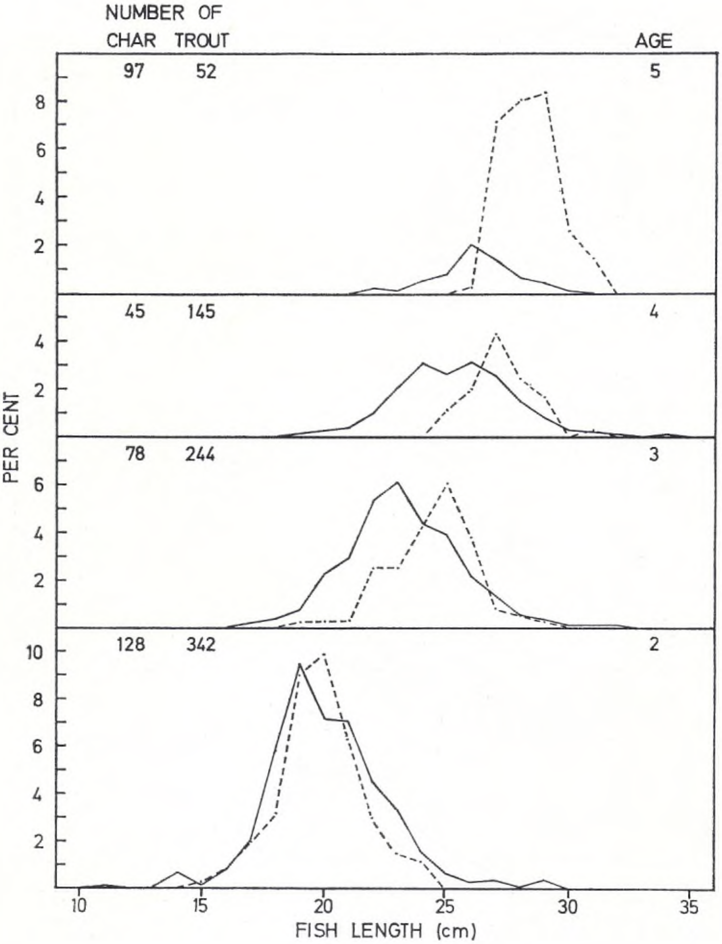

Fig. 4. Length-frequency distribution of char, *Salvelinus alpinus* (L.), (------) and brown trout, *Salmo trutta* L., (———) caught from September 1972—June 1973 in Lake Løne, Western Norway.

Fecundity

As a measure of the reproductive capacity in relation to body size, the regression of the individual fecundity on body length is given in Fig. 5. Larger fish have on average more eggs than do smaller ones. The fecundity of the char is also significantly higher than that of brown trout in Lake Løne, tested as proposed by SNEDECOR and COCHRAN (1967, p. 432—436). The data for the fecundity of the Løna trout with body lengths between 19.5 and 32.5 cm are given by JONSSON (1977).

The fecundity of the Løna char is close to the results found by MÄÄR (1949) for char spawning in stony streams in northern Sweden. The Løna char spawn in shallow waters (depth 1—5 m) within a limited area of the lake. In recent years the spawning ground has been covered by a layer of fine grained mud. Inspection by scuba diving showed no locations with grawel, only mud-covered rocks and soft bottom with *Isoëtes lacustris* and *Spongilla lacustris*.

IV. DISCUSSION

Growth strategy

Within each age group, the length distribution of the Løna char is more homogeneous than is that of the Løna trout. The difference is most striking in the oldest age groups. The char appear to mature sexually at a specific length, usually about 26—28 cm. Growth stagnation after their first spawning season may lead to more uniform length distribution with increasing age. The brown trout is not uniform in the same way, probably owing to their rather variable length when reaching sexual maturation (JONSSON 1977).

A more uniform length distribution within the various age groups of char compared with trout as found in Lake Løne appears to be a fairly general tendency in localities where the two species live sympatrically (SCHMIDT-NIELSEN 1939, SVÄRDSON 1949, FILIPSSON and SVÄRDSON 1976), and cannot be explained only by the differences in reproductive strategy. The explanation may also lie partly in their different behaviour, habitat, and diet.

The char are generally found to have a tendency to roam, often forming schools, and they do not show much aggressiveness except during spawning time (FABRICIUS and GUSTAFSON 1954, NILSSON 1963, 1965, FILIPSSON and SVÄRDSON 1976). This appears also to be the case for the Løna char. Like most populations of sedentary char (AASS 1968), the Løna char are lake dwellers throughout their entire life span, completely independent of running waters. Char in age groups 1—2 live mainly in the deeper parts of the lake, feeding largely on zoobenthos. Older char live to a large extent pelagically. They appear primarily to feed on zooplankton (MATZOW 1976, JONSSON and MATZOW 1979, ch. 7).

The brown trout are generally found to be markedly territorial (KALLEBERG 1958, NILSSON 1963, 1965, FILIPSSON and SVÄRDSON 1976). Like most other trout populations, the Løna trout are hatched in streams, where they usually live for 1—2 years before migrating to the lake. There, they primarily occupy the littoral zone and the upper strata of the pelagic zone of the lake. They may return to the stream for feeding in spring and spawning in autumn (JONSSON and MATZOW 1979). The trout feed on zoobenthos, terrestrial insects, zooplankton and fish (MATZOW 1976, JONSSON and MATZOW 1979, ch. 7).

The difference in behaviour, habitat, and diet may lead to greater individual variation in growth rate in populations of brown trout than in char. However, the different length distributions cannot fully be explained by this. SVÄRDSON (1949) found experimentally that trout had a more variable growth rate even when the two species were reared together in a trough, all fed with liver. In his experiment, the char occurred in higher density than the trout, and he suggested that the difference might be an effect of a different degree of intraspecific competition within the two species. This hypothesis, however, appears unlikely as a general explanation, as the same tendency is observed both in localities where the char are numerically superior and in localities where they are numerically inferior compared with the trout. It appears more probable to the present authors that the difference in length distribution between the two species is partly due to natural selection. As the habitat of the char at least in the southern part of its distribution area usually is much more uniform than that of brown trout, it may in this area be expected that the char may be more specialized, both genotypically and phenotypically (MAYR 1963, FRYER and ILES 1969, VALENTINE 1976). Experiments on the oxygen metabolism in different char populations further indicate a high degree of population specific isolation and specialization (ROSSELAND 1977). The trout, being adapted to both lentic and lotic habitats during its life span, may have a more generalized geno- and phenotype. The difference in growth strategy between char and trout may also, however, be directly influenced by differences in behaviour,

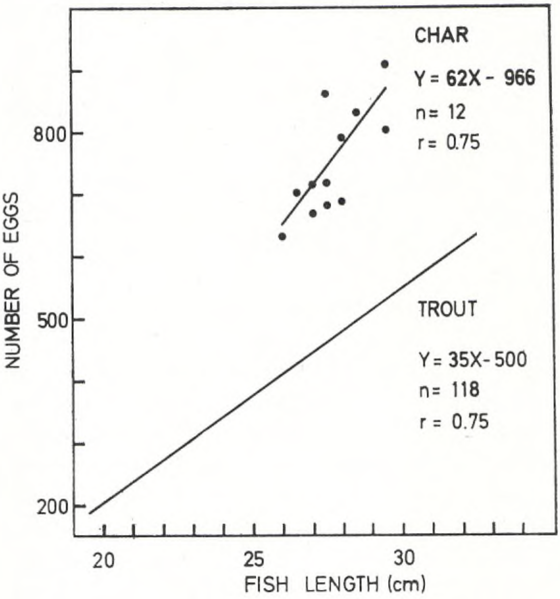

Fig. 5. Regression of number of eggs per female (individual fecundity) on fish length of char, *Salvelinus alpinus* (L.), and brown trout, *Salmo trutta* L., caught in Lake Løne, Western Norway.

habitat, diet, and reproductive strategy between the two species.

Reproductive strategy and year-class fluctuations

The reproductive strategies of char and brown trout in Lake Løne appear rather different. The age and size of the char when reaching sexual maturation are fairly uniform. This is probably mainly a consequence of the uniform growth rate and length of life span in the char population. As for the brown trout, it may be expected that the age at sexual maturation is a function of the net reproductive rate (R), in order to maximize the number of highly viable progeny in the long run (JONSSON 1977). But, while most of the Løna trout apear to breed only once before dying, the Løna char may often breed repeatedly. In this way the recruitment of the char population is buffered against disadvantageous fluctuations. In the Løna trout, the recruitment is stabilized by a very heterogeneous age and size at sexual maturation. For char, the net reproductive rate may be estimated from the formula

$$R = \sum_{x=a}^{b} l_x f_x,$$

where a designates the age when sexual maturation is reached, b the length of the life span, l_x the age-specific survival rate, and f_x the age-specific individual fecundity.

Although the char is iteroparous, and thus should be shielded against severe fluctuations in recruitment, the material indicates that every third year gives rise to a rather strong age group, while no similar year-class fluctuation has been observed for the Løna trout. Regularly fluctuating year-class strength has been demonstrated in many species, both among freshwater fishes (*e.g.* MONASTYRSKY 1940, ALM 1952, AASS 1972) and also, and even more frequently, among marine fishes (*e.g.* HANSEN and NANSEN 1909, HJORT 1914, 1926, JENSEN 1927, 1933, 1954, ROLLEFSEN 1954). Such fluctuations have often been correlated with variations in abiotic factors (*e.g.* HANSEN and NANSEN 1909, JÄRVI 1942 a, b, SVÄRDSON and MOLIN 1968), or with human exploitation (HUITFELDT-KAAS 1917). However, according to several authors (*e.g.* JENSEN 1933, 1954, NIKOLSKY 1963, 1969, AASS 1972), changes in feeding conditions more often give a satisfactory explanation of this phenomenon. This factor also seems to provide a rational explanation of the results from Lake Løne.

In char, the youngest age groups appear to compete largely for zoobenthos (MATZOW 1976). Age group 0 is lacking in the material, but the finger marks on the back of fry of reared Løna char, and sampling of char fry in other localities (KIRCHEIS 1976, JONSSON and MATZOW 1979, p. 20) indicate that they live a benthic way of life. From age group 3 on zooplankton seems to be the more important food (MATZOW 1976). By competing for food, a strong year class will suppress the next two year classes; every third year when the strong year class releases its predation pressure on zoobenhtos, a new strong year class will emerge. In this way, the three-year cycle may have been formed.

Among brown trout, a large part of the fry migrate to the lake after one year in their nursery area, and only a few individuals appear to stay more than two years in the river. In the lake, the youngest trout are usually found high up in the littoral zone while the older age groups are often found somewhat deeper in the littoral zone and in the upper strata of the pelagic zone (MATZOW 1976, JONSSON and MATZOW 1979, ch. 7). Both in lentic and lotic conditions, young trout are found to be territorial (KALLEBERG 1958, NILSSON 1963). This secures a rather stable population density. The different spatial distribution between different age groups lessens the intraspecific competition for food, and together with the territoriality it secures a relatively even recruitment each year.

The hypothesis is thus that for the Løna char intraspecific competition for food in the first three years leads to a strong year class every third year. For the Løna trout, competition for food is decreased by a different spatial distribution between the various age groups. This, together with territoriality, gives a fairly constant recruitment each year.

V. SUMMARY

1. In Lake Løne, the char *(Salvelinus alpinus* (L.)) have a more homogeneous length distribution in all age groups than the brown trout (*Salmo trutta* L.). This appears to be a consequence of differences in behaviour, habitat, diet, and reproductive strategy.

2. The char are of rather uniform age and size at sexual maturation compared with the brown trout. The char appears usually to spawn at least twice (iteroparity), while most of the brown trout appear to spawn only once in Lake Løne (semelparity).

3. Although the char are iteroparous, and thus shielded against disadvantageous fluctuations in recruitment, the material indicates that strong year classes are formed every third year. No similar year-class fluctuations have been observed for the brown trout. For char, the year-class fluctuations may be due to intraspecific competition for food among age groups 0—2. For brown trout, year-class fluctuation may be prevented by territoriality and a different spatial distribution between the various age groups.

4. The individual fecundity is significantly higher for char than for brown trout.

VI. ACKNOWLEDGMENTS

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The Habitat of Perch *Perca fluviatilis* L. on the Outskirts of its Swedish Distribution, Lakes and Lake Reservoirs

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CONTENTS

I. INTRODUCTION

Perch populations occur in a wide range of habitats in Europe. The feeding habits are usually described as being a sequence of three stages, starting with zooplankton feeding and ending with predation on fish, although plasticity is reported in this character too.

One approach to an analysis of perch distribution is by way of a study of the tolerance of the species to different factors, and particularly the survival of eggs and young over "critical stages". In some respects perch is a tough species. It can endure an acid environment better than many other species (ALMER *et al.* 1974, MILBRINK and JOHANSSON 1975). For some other factors, such as temperature and oxygen levels, perch shows an intermediate tolerance (VARLEY 1967, pp. 29—52, for temperature tolerance in egg, larval and early young stages see also SWIFT 1965, HOKANSON and KLEINER 1974). To VARLEY's analysis of many factors influencing the distribution of fishes there could be added, for anyone specifically desiring to obtain a good insight into the limitation of perch distribution in cold climates, the more recent analysis of CHRISTIE and REGIER (1973) of temperature as "a major factor influencing the reproductive success".

Another, quite different approach is used by TESCH (1955), who studied the growth and yield of perch in Central European lakes to get information on the optimal condition for perch populations. He states that optimal conditions are given in "alternden Maränenseen bis werdenden Bleiseen mit gutem Stint- und Plötzenbestand". TESCH considers it to be an important precondition for the production of high perch yields, that there should exist appropriate quantities of littoral fauna and available prey fish offered in the appropriate period of the life history of the perch. Where these conditions are not satisfied, as in small lakes and tarns and waters very rich in vegetation, the perch is stunted or the populations are sparse. Dense populations with stunted growth are still successful in an ecological sense, even if no yield is taken by man. When the conditions are suboptimal in other ways, sparse populations with poor growth are obtained. Here the situation in the Central European coregonid lakes is of particular interest: the more oligotrophic the lakes are, the smaller the littoral zones of the lakes and the more important the coregonid populations, the smaller is the yield from the perch populations. Such lakes constitute a transitional group towards alpine conditions, a parallel to the situation in the present study in some respects.

Perch is one of the most important fish species in Sweden, and the biology of populations in small lakes and tarns and the limit of perch distribution in the Baltic has been treated by ALM (1946, 1952, 1954, 1957, 1959, 1960) and, more recently, in a

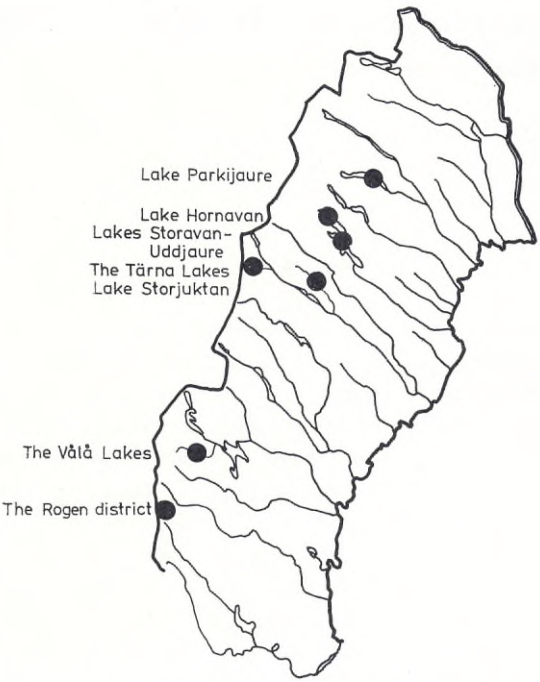

Fig. 1. Northern Sweden with the lakes studied.

number of mimeographed papers by KJELLBERG (1971), NEUMAN (1974 a, b), NYBERG (1976) and LESSMARK (1976); *cf.* NEUMAN (1979 a and b) in this volume and PERCIS (1977) too. In the present study, some oligotrophic North Swedish lakes and lake reservoirs are classified according to proximity to the high mountains and certain other general characteristics, including competing species. The habitat and growth of perch in these lakes and lake reservoirs will be studied in relation to the environment on the outskirts of perch distribution and particularly in relation to the temperature factor.

II. GENERAL CHARACTERISTICS OF THE LAKES AND MATERIAL AND METHODS

On the outskirts of its distribution, close to the high mountains, perch occurred together with char and trout in the Tärna lakes (alt. 377—89 metres) and with these species and burbot, pike, grayling and minnow as well in the Vålå lakes (alt. 450—80 metres). The perch in the catch was sometimes of small size.

Further down in the North Swedish inland are two lakes with perch, whitefish, trout, pike, burbot, grayling and minnow, Lake Parkijaur (alt. 292 metres) and Lake Storjuktan (alt. 399 metres, Map, Fig. 1). Whereas the Tärna and Vålå lakes could be termed char lakes after the originally dominating fish species, Lake Parkijaur and Storjuktan are termed whitefish lakes (LINDSTRÖM and FILIPSSON 1972, BERGSTRAND 1977).

In the 1920s whitefish was introduced into the Tärna lakes by man. The regression of the char populations has been fairly slow, probably because of the cold climate. During the course of the investigation all the lakes discussed were converted into lake reservoirs, and so the investigation can also serve as a first approach to a study of the perch niche in a lake reservoir.

Table 1 reports the composition of the fish catches and Table 2 the number of gill-net efforts and total catch in the test fishing.

The investigation is based mainly on catch per unit effort with gill nets. Catch per unit effort was never intended as an estimate of absolute abundance in future lake reservoirs in Sweden (mimeographed paper in Swedish, LINDSTRÖM 1960), but it should be used as an index that could be compared with other indices obtained under similar circumstances (RUSSELL 1931). The recognition of relevant characteristics of "similar circumstances" depends on our knowledge of fish behaviour in the presence of the gear, of the activity and the statistical distribution of fish and of the handling of the gear, and this knowledge is continuously increasing. A recent paper on the thermobiology of perch populations in the vicinity of nuclear power plants has emphasized the importance of perch activity at different temperatures (NEUMAN 1974 a, 1979 b), and this will render comparisons between gill net catches from different depths and different lakes difficult. There is also, of course, an interrelation between catch per unit effort and total yield, and, given a certain level of fishing, the catch per unit effort will tend to decrease with increasing total yield. The Tärna lakes and other lakes in Northern Sweden do follow the Morphoedaphic

Table 1. *Composition of fish catch in the lakes in natural state, weight percentages, and areas of the lakes in square kilometres.*

Lakes	Trout	Char	Grayling	Whitefish	Perch	Pike	Burbot		Square km	Total yield kg/ha
Parkijaur	1	—	1	32	50	14	2	a	19	
	3	—	7	60	15	15	0	b		≥0.5
Storjuktan	8	—	5	58	16	11	2	b	26	6.4
The Tärna lakes										
Outflow from Lake Ö. Björkvattnet to outflow from Lake Vojtjajaure	44	49	—	—	7	—	—	b	—	5.2
Outflow from Lake Votjajaure to outflow from Lake Nedre Björkvattnet	20	23	—	54	3	—	—	b	—	
The Vålå lakes										
Aumen	29	16	1	—	27	20	7	a	4	2.5
Hottön	56	15	0	—	9	13	7	a	7	
Gesten	53	18	0	—	19	0	10	a	1	
Håckren	29	16	1	—	41	0	13	a	2	

The composition of the fish catch is obtained either from a fishing organized by the Drottningholm laboratory with a graded gang of gill nets (a), or from a total yield report from the fishermen (b). The latter have a diversified collection of gear at their disposal and use the gear for a selective fishing for preferred species.

Index (RYDER *et. al.* 1974) when arranged according to species composition (Fig. 2), and this is an indication that the lakes are at least moderately fished. There is thus every reason to take into account total yield data as well. Long experience has enabled man to exploit a good perch population wherever such a population exists. Perch is not, however, particularly fished for in these lakes, with the exception of the tarn Lake Stensjön in the Tärna district (*vide infra*). On the contrary, the fishing is generally directed to salmonoid fishes.

Thus there is little justification for a comparison of catch per unit effort between lakes. In the present study each lake is studied with regard to variation in catch per effort between habitats, depths and mesh sizes within the lake.

III. DEPTH DISTRIBUTION

There seem to be certain trends in the gill-net catches.

(1) Lake Parkijaur. All eight sections are not fished at all three depths with all seven mesh sizes (Figs. 3 and 4). The depth distribution described below could be counterfeited at sections 5 and 6 in 1970 and section 9 in 1975, where an inspection of the material reveals a deeper setting of the successful mesh sizes in the autumn. The general trends illustrated in the figures are, however, higher catches in gill nets between 1 and 5 metres than in those below 5 metres total depth in summertime (July) and a lower centre of depth distribution in September.

(2) Lake Storjuktan. A ranking of all cases (as 1: 0, 0: 1 or 1/2: 1/2) where a mesh category is used between 1 and 5 metres as well as below 5 metres within each section and season reveals a slightly shallower centre of depth distribution in July—mid-August than in June or in mid-August —September. Higher ranking points are obtained for 1—5 metres than for nets below 5 metres in all three seasons (Table 3). When catch per net is studied instead of the ranking points only, the

Table 2. *Bulk of the material studied, number of gill nets and number of fish.*

		Season I			Season II			Season III		
Lakes	Year	Units of gill-net efforts	Perch	Other species	Units of gill-net efforts	Perch	Other species	Units of gill-net efforts	Perch	Other species
Parkijaur	1970	—	—	—	63	301	440	63	277	348
	1975	—	—	—	63	398	214	63	321	233
Storjuktan	1957 1958 1959 1961	541	721	774	1,145	1,232	1,466	672	621	1,433
	1967	110	111	1,229	—	—	—	198	772	1,736
Aumen	1957	156	285	214	117	165	228	—	—	—
Hottön	1957	180	65	302	162	173	404	—	—	—
Gesten	1957	72	49	96	72	189	205	—	—	—
Håckren	1957	90	339	76	72	164	114	—	—	—
The Vålå lakes	1957	498	738	688	423	691	951	—	—	—
Aumen	1958	144	126	253	144	96	156	—	—	—
Hottön	1958	168	43	180	172	78	275	—	—	—
Gesten	1958	72	55	77	72	34	111	—	—	—
Håckren	1958	90	150	70	90	101	61	—	—	—
The Vålå lakes	1958	474	374	580	478	309	603	—	—	—

Parkijaur:	A gang of monofilament gill nets with knot-to-knot measure (bar measure) 50.0, 37.5, 33.0, 30.0, 25.0, 21.4 and 16.7 mm.
Storjuktan:	Gill nets of spun nylon with the same mesh sizes as in Lake Parkijaur but with a representation shifting during the years.
The Vålå lakes:	Monofilament and spun nylon gill nets with the same mesh sizes as in Lake Parkijaur, but with twice as many 30 mm and 33 mm nets as other net categories.

Pelagic gill nets are not included in this table.

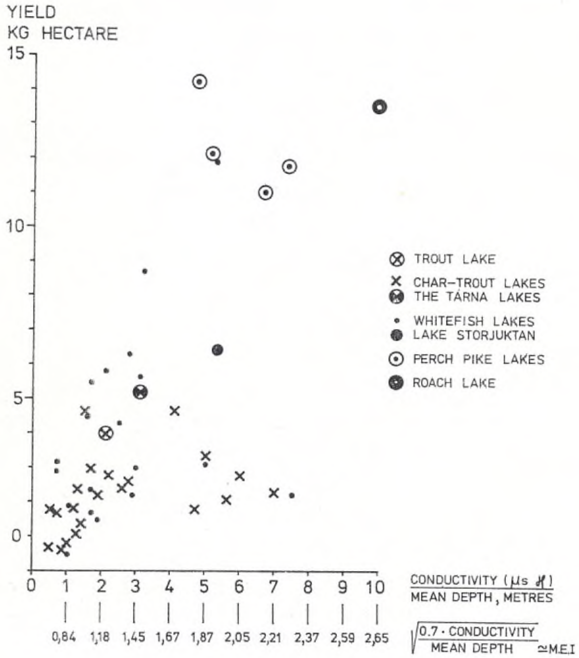

Fig. 2. Morphoedaphic index against yield from a number of North Swedish lakes, grouped according to dominating fish species (*cf.* symbols). The TDS exchanged for 0.7 x conductivity. (Full presentation in a mimeographed memorandum to the Fishery Board of Sweden October 10, 1975.)

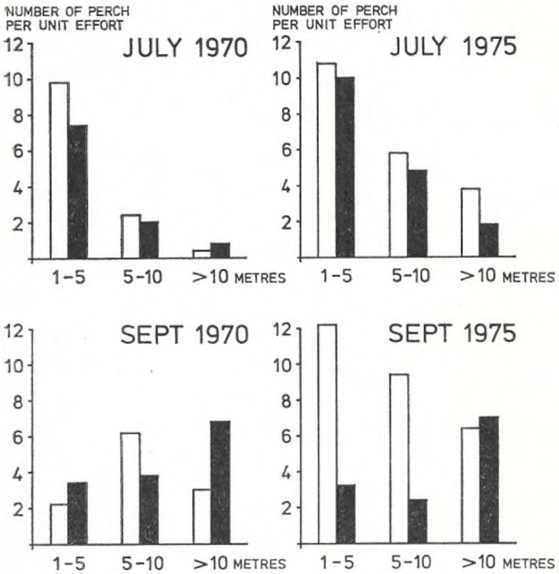

Fig. 3. Lake Parkijaure, depth differences in number of perch per unit gill-net effort. White columns, mean for two small-meshed nets (knot to knot 17 and 21 mm), and black columns mean for five coarse-meshed nets in the gang of seven different nets (mesh sizes 25, 30, 33, 38 and 50 mm).

difference between the two depths seems less convincing in 1967. By 1967 the lake had been a reservoir for five years. A new method of handling the gill nets sheds some light on the depth distribution. A long gang of gill nets was set on the bottom with all seven mesh sizes represented, from the shore towards the middle of the lake, in section 6, in June as well as in August—September. The bottom fell off fairly rapidly at this place and most of the 54 nets occurred below 10 metres total depth. Perch catches in this long net gang were few, thirteen perch altogether, the highest catch being 7 perch in a net about 20 metres total depth (Lindström 1967). The transformation into a reservoir may have brought about a deeper occurrence of perch catches.

(3) In two of the Vålå lakes the perch is concentrated in shallow sections where there is no depth greater than 5 metres (Skåltjärn in Lake Aumen, the NW bay of Lake Gesten). In most of the other sections perch was scarce, both above and below 5 metres. Only in Lake Håckren, where all bays are of "inshore" character, is it possible to calculate a depth distribution by simple comparisons within sections. More perch were caught in Lake Håckren below 5 metres than between 1 and 5 metres in July and September 1957 and more above 5 metres in July 1958 (Table 4). The discrepancy between the July catch in Lake Håckren 1957 and most of the other data in this study is difficult to understand. The catch per net in Lake Håckren fluctuates wildly, like most other perch catches in this study, and the inverse depth distribution in July 1957 is mainly the effect of catch in two nets. Such a clumped distribution is typical of most of the perch catches studied and it makes it difficult to attain significance for any tested trend.

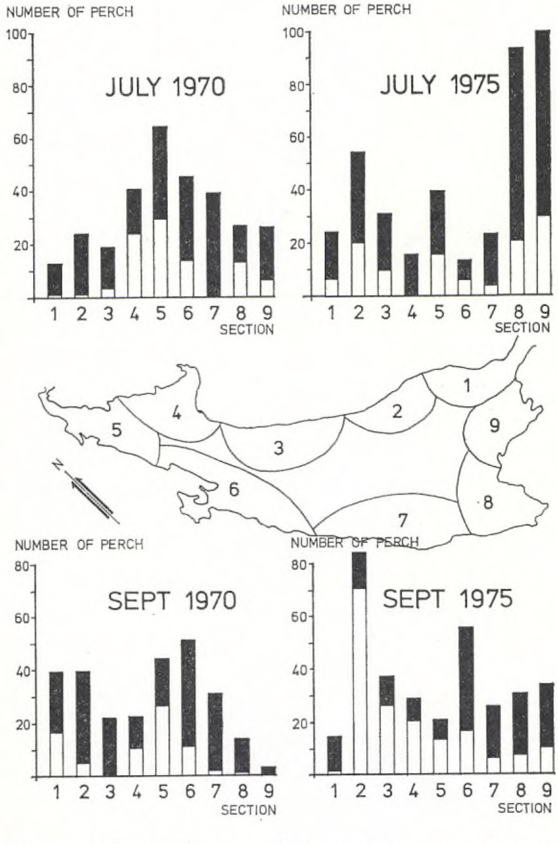

Fig. 4. Lake Parkijaure, differences between sections in number of perch per one gang of 7 gill nets in different mesh sizes. The white part of the columns represents the cath in mesh sizes 17 and 21 mm knot to knot, the black part the catch in the coarse-meshed nets, 25, 30, 33, 38 and 50 mm knot to knot.

Table 3. *Lake Storjuktan. Sums of ranking points above or below 5 metres for all sections fished in both depth ranges, based on means of perch catch (in number) per unit effort. Ranking results are noted either as 1: 0 or 0: 1 or 1/2: 1/2. A mean is calculated for all nets pooled together from one season, one year, one mesh category and one section.*

mesh size depth		17 mm		21 mm		25, 30, 33, 38, 50 mm	
		≤ 5 m	> 5 m	≤ 5 m	> 5 m	≤ 5 m	> 5 m
June	1958	2 1/2	1/2	1	2	8	7
	1959	—	—	0	1	3	7
	1961	—	—	—	—	5 1/2	1 1/2
	1967	2 1/2	2 1/2	2	1	1 1/2	1 1/2
Total		5	3	3	4	18	17
July—early August	1957	4 1/2	1 1/2	4	0	13 1/2	6 1/2
	1959	—	—	—	—	4 1/2	4 1/2
	1961	—	—	—	—	3	5
Total		4 1/2	1 1/2	4	0	21	16
Late August—September	1958	2	0	1 1/2	2 1/2	7 1/2	6 1/2
	1959	—	—	—	—	5 1/2	9 1/2
	1961	—	—	—	—	5 1/2	3 1/2
	1967	2	3	3	2	9 1/2	4 1/2
Total		4	3	4 1/2	4 1/2	28	24

After the Vålå lakes were transformed into a single lake reservoir in 1966, the Lake Håckren reservoir, a fishing with survey bottom nets with all seven mesh sizes included in each net was performed down to 65 and 60 metres respectively in August 1972 and 1973. The catches were concentrated within 5—15 metres total depth, where 48 perch were caught in six nets as compared with 0 perch in seven nets in other depths. Such gangs of gill nets were not employed when the Vålå lakes were in a natural state, but the results nevertheless add some support to the hypothesis that perch occur at greater depth in a lake reservoir than in the natural lake, when compared with results from Lakes Parkijaur and Storjuktan.

To sum up, the catches of perch between 1 and 5 metres in summertime are higher than they are below 5 metres in natural lakes and the centre of depth distribution of the catch is deeper in September than in July (Parkijaur) and deeper in June and late August—September than in July—early August (Storjuktan). The material from the Vålå lakes is somewhat inconsistent. The general trend in depth distribution when lakes have been reservoirs for some time may possibly be a deeper appearance of the catches.

Considering the strong influence of the activity of the perch on the gill-net catches, one should not place too much reliance on any of the discussed differences as a true measure of differences in perch abundance.

IV. DIFFERENCES BETWEEN SECTIONS WITHIN THE LAKES

The differences between sections in Lake Parkijaur are analysed in a similar way to the differences between depth. The sections are fished with one set of standardized gill nets each. Where the differences illustrated in Fig. 4 a—d could be "counterfeited" by interplay between sections and depth differences in perch abundance in any section, that section has been discarded. The treatment leaves sections 2 and 8 as the most promising ones, but they then behave very differently in 1970 and 1975. The high catches in section 2 in autumn 1975 came from a single net and section 8 was much affected by preparations

Table 4. *The Vålå lakes. Number of perch per unit effort in different gill nets and different parts of the lake system. Skåltjärn and Gesten NW are shallow parts with no nets deeper than 5 metres (Map, Fig 6, depth partly in* LINDSTRÖM *1952, 1957). Catch is not always specified as to depths in the material. Mesh sizes: 17 and 21 mm knot to knot and coarse-meshed=mean of means for the mesh-size categories 25, 30, 33, 38 and 50 mm knot to knot.*

	Mesh 17 mm	Mesh 21 mm	Coarse-meshed	Units of gill-net effort	Mesh 17 mm	Mesh 21 mm	Coarse-meshed	Units of gill-net effort	Mesh 17 mm	Mesh 21 mm	Coarse-meshed	Units of gill-net effort	Mesh 17 mm	Mesh 21 mm	Coarse-meshed	Units of gill-net effort
Lake	Skåltjärn				Rest of Aumen				Skåltjärn				Rest of Aumen			
Season	June 1957				June 1957				August 1957				August 1957			
Depth 1—5 m	3.5	42.0	10.9	18	2.6	2.9	0.1	107	10.0	53.0	6.1	8	2.3	1.4	0.3	94
Depth 5—10 m					0.5	0.0	0.0	24				1	0.0	0.0	0.0	13
All depths	3.5	42.0	10.9	18	1.8	2.3	0.1	138	10.0	53.0	6.6	9	2.1	1.2	0.3	108
Lake	Skåltjärn				Rest of Aumen				Skåltjärn				Rest of Aumen			
Season	June 1958				June 1958				August 1958				August 1958			
Depth 1—5 m	0.0	5.0	6.8	18	0.5	1.0	0.2	114	0.0	0.0	5.1	18	0.4	0.6	0.1	103
Depth 5—10 m					0.0	0.0	0.7	12					0.0	0.0	0.0	19
All depths	0.0	5.0	6.8	18	0.4	0.9	0.2	126	0.0	0.0	5.1	18	0.3	0.6	0.1	126
Lake	Hottön				Hottön				Hottön				Hottön			
Season	June—July 1957				June—July 1958				August 1957				August 1958			
Depth 1—5 m	3.0	0.5	0.1	137	0.5	1.1	0.1	133	3.5	5.5	0.1	125	Not specified as to depths			
Depth 5—10 m	0.9	0.7	0.1	40	2.2	0.3	0.0	29	5.0	2.8	0.4	33				
All depths	2.2	0.6	0.1	180	1.1	0.8	0.1	168	3.9	4.8	0.1	162	1.1	2.2	0.2	172
Lake	Gesten NW				Rest of Gesten				Gesten NW				Rest of Gesten			
Season	June 1957				June 1957				August 1957				August 1957			
Depth 1—5 m	15.0	2.5	0.2	16	7.5	0.0	0.0	44	50.5	23.0	1.25	17	3.8	4.8	0.2	46
Depth 5—10 m	5.0		0.0	2	1.5	0.0	0.0	10		0.0		1	0.0	3.0	0.0	8
All depths	10.0	2.5	0.2	18	3.5	0.0	0.0	54	50.5	11.5	1.25	18	2.5	4.2	0.2	54
Lake	Gesten NW				Rest of Gesten				Gesten NW				Rest of Gesten			
Season	July 1958				July 1958				August 1958				August 1958			
Gesten NW not over 5 m deep, otherwise depth not specified	18.0	5.0	0.4	18	0.8	0.8	0.2	54	2.0	3.0	0.0	18	1.5	0.8	0.2	54
Lake	Håckren				Håckren				Håckren				Håckren			
Season	July 1957				July 1958				First in September 1957				August 1958			
Depth 1—5 m	19.7	6.4	0.5	72	2.4*	5.4*	1.7*	57*	10.0	2.6	1.0	64	Not specified as to depths			
Depth 5—10 m	5.5	42.5	0.9	16	0.0*	0.0*	1.1*	12*	16.0	10.0	0.8	7				
All depths	14.0	16.6	0.6	90	1.2	3.8	1.6	90	10.0	9.5	1.1	72	1.5	21	1.0	90

* Only partly specified as to depths

Table 5. *Sums of ranking points for the perch catches in different sections of Lake Storjuktan. Eight sections and single ranking points from 1 to 8. Mean of number perch per unit effort in each of the two most fine-meshed gill nets and mean of mean of the five more coarse-meshed gill nets in a season and year constitutes the material qualifying for the ranking. Some fishing in all sections with all mesh sizes in required. To avoid influence from depth, only nets from 1—5 metres (in 1967 1—10 metres) are used for the comparison.*

Years	Sections:								
	Ia	II	III	IV	V	VI	VII	VIII	
1957—58—59—61	29 1/2	38 1/2	35 1/2	32 1/2	33 1/2	48	29	41 1/2	Mesh size 21 and 17 mm, four periods (years, seasons)
	135	170	190	210	145	170	192 1/2	227 1/2	Mesh size 25, 30, 33, 38, and 50 mm, eight periods (years, seasons)
Total	164 1/2	208 1/2	225 1/2	242 1/2	178 1/2	218	221 1/2	269	
1967	21 1/2	16	18	20	15 1/2	16	13 1/2	23 1/2	Mesh sizes 21 and 17 mm, two seasons
	65	55	75	45	17 1/2	40	12 1/2	50	Mesh sizes 25, 30, 33, 38 and 50 mm, two seasons
Total	86 1/2	71	93	65	33	56	26	73 1/2	

for the dam construction in 1970 (as section 9 also was). Inlet and outlet sections (1 and 5) show mediocre catches with the exception of the 1970 summer catch in the shallow section 5. No consistently preferred section can be noted in Lake Parkijaur.

The sections in Lake Storjuktan are ranked according to perch catches in the depth 1—5 metres in the years 1957, 1958, 1959 and 1961 and the catches in the depth 1—10 metres in 1967, Table 5. (The depth analyses seem to indicate that it would be reasonable to expand the depth studied in 1967.) In accordance with the outcome, sections Ia, III, V, VII and VIII are chosen as being the most interesting (high or low ranking points) and numbers of perch per unit effort are tabulated in Table 6 for several more seasons and with two extra sections included in the totals, (Map, Fig. 5). The main inlet section VII shows medium or low values, as also does the outlet section Ia before the lake reservoir was constructed. In 1967 section Ia is one of the best, being now separated from the new exit by a section added through the impoundment, Ib. Sections VIII and III are on average good and section V is "bad". Of the selected five sections, four are situated close to running water, but the brooks entering section VIII and III differ in some respects from the main inlet. Temperature observations are missing but the brooks come from the vicinity whereas the main inlet (VII) comes from a precipitation area starting in the high mountains ~ 50 kilometres away and passing *e.g.*, through two lakes of the same size as Lake Storjuktan before entering that lake. These facts should correspond to a temperature difference that could be responsible for the catch difference. Differences in stream velocity could also be important.

Perch occurrence will now be described in two regions close to the high mountains.

In the Håckren lakes fishing was carried out during the years 1957—60, the years 1957 and 1958 giving higher totals as well as higher perch catches (Table 7). The difference in totals is mainly an effect of a change in the set of gill nets

Table 6. *Number of perch per unit gill-net effort in certain sections in Lake Storjuktan. The figures entered are means for three seasons (June, July—early August and late August—September) in the years 1957—61, and means for only two seasons in 1967. All material from one section, one mesh size and one season is first pooled and catch per net calculated, a mean is computed for the coarse-meshed net categories and ultimately a mean for the entering seasons is formed, giving the figures in the table.*

Years	Mesh size, mm, knot-to-knot measure	Sections:					All Fished sections
		Ia	III	V	VII	VIII	
1957—59	17	1.23	6.50	2.33	2.56	4.81	4.15
1957—61	21	2.56	1.74	6.29	2.44	5.77	3.11
1957—61	25, 30, 33, 38 and 50	0.61	0.93	0.83	1.43	1.91	1.01
1967	17	7.83	4.25	3.00	3.13	6.88	4.50
1967	21	8.00	8.50	4.67	2.00	9.13	4.51
1967	25, 30, 33, 38 and 50	6.50	19.25	0.75	0.75	6.63	4.27

employed — fewer fine-meshed nets in 1959—60. The difference in perch catches is partly an effect of the change in gear but also partly of some change in, *e.g.*, the size structure of the perch population (Chapter VI), as some perch of good size were obtained in 1958. The years 1957 and 1958 are chosen for a closer investigation, as the set of gill nets was more diversified in these years.

The perch catch varies considerably between sections. A standardized set of gill nets (with 7 mesh sizes) used in Lakes Aumen, Hottön and Gesten in 1957 gave a catch per net as low as 0.5, if 18 out of 753 nets are disregarded. These few nets, chosen *a posteriori* on the merit of their high catches, raise the mean catch per unit effort to over 1.0 when included. The sections with these successful nets were as follows: (1) Skåltjärn, an

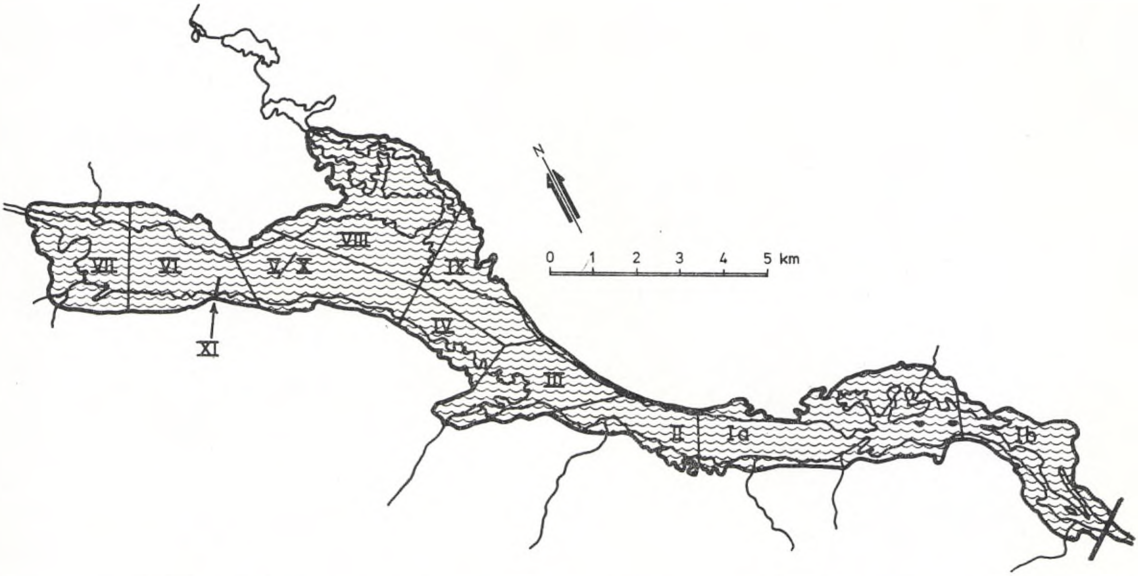

Fig. 5. Map of Lake Storjuktan as a lake reservoir with the old shore indicated by a thin line. Numbers indicate sections.

Table 7. *Survey netting in the years 1957—60 in the Vålå lakes: catch per unit effort in number. Two seasons, early summer and late summer with a break after July 20. The fishing started in 1957 and 1958 with nylon gill nets in the standardized gang of different mesh sizes, described in Table 2, but later the mesh-size composition changed, as discussed in the text, towards more coarse-meshed nets. Catches from particular "perch sections" in 1957 and 1958 are described in Table 4.*

		Lake Aumen			Lake Hottön			Lake Gesten			Lake Håckren		
Year	Season	Perch, catch per unit effort	Catch per unit-effort, all species	Number of gill-net efforts	Perch, catch per unit effort	Catch per unit-effort, all species	Number of gill-net efforts	Perch, catch per unit effort	Catch per unit-effort, all species	Number of gill-net efforts	Perch, catch per unit effort	Catch per unit-effort, all species	Number of gill-net efforts
1957	Early	1.8	3.2	156	0.4	2.0	180	0.7	2.0	72	3.8	4.6	90
	Late	1.4	3.4	117	1.1	3.6	162	2.6	5.5	72	2.3	3.9	72
1958	Early	0.9	2.6	144	0.3	1.3	168	1.0	1.8	72	1.7	2.4	90
	Late	0.7	1.8	144	0.5	2.1	171	0.5	2.0	72	1.1	1.8	90
1959	Early	0.4	1.2	300	0.1	0.6	450	—	—	—	—	—	—
	Late	0.1	0.9	443	—	—	—	0.4	3.4	150	1.0	1.9	299
1960	Early	0.1	1.1	290	0.2	1.7	296	—	—	—	—	—	—
	Late	0.0	1.4	539	—	—	—	0.1	1.2	270	0.6	1.9	300
Selected catches "Perch sections"													
1959	Early	4.4	5.4	20	—	—	—	—	—	—	—	—	—
	Late	—	—	—	—	—	—	1.2	2.4	30	—	—	—
1960	Early	0.6	1.7	21	—	—	—	—	—	—	—	—	—
	Late	—	—	—	—	—	—	1.0	2.7	20	—	—	—

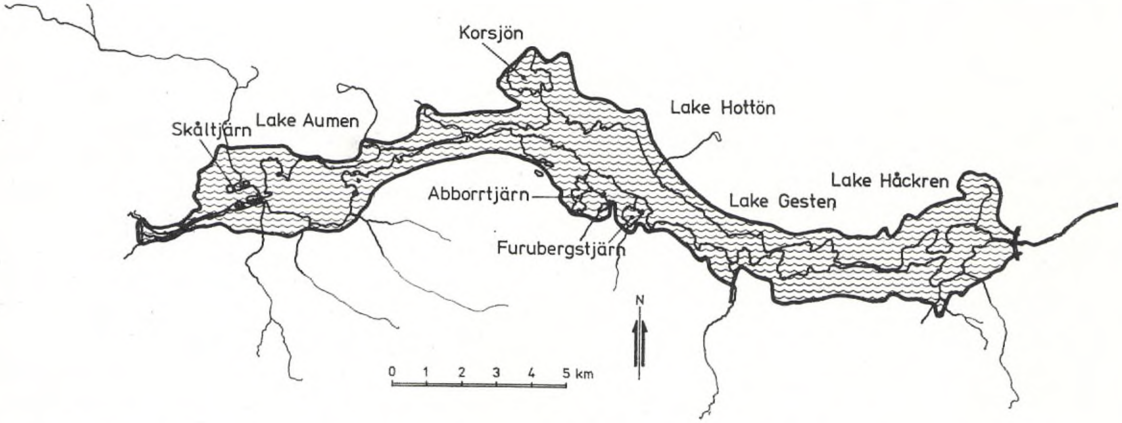

Fig. 6. Map of the Vålå lakes and the Lake Håckren reservoir. The old shore is indicated by a thin line.

extension of a minor tributary to Lake Aumen, close to the lake, (2) just beyond the point where a brook running from Lake Abborrtjärn (the "perch tarn") flows into Lake Hottön, and (3) downstream of the main inflow into Lake Gesten (Map, Fig. 6), shoreward from a large eddy and an important clump of *Potamogeton* and *Myriophyllum.* Furthermore, the perch catches are good in (4) Lake Håckren, a lake formed by several small bays, *cf.* the map. Features common to the rich localities are: closeness to running water and a position often somewhat detached from large open basins — a comparison between the configuration of Lakes Håckren and Hottön and their perch catches can give an idea of the difference between a rich and a poor perch locality.

Two small tarns which were connected to Lake Hottön by brooks constitute exceptions from the pattern. They were fished in 1957 and 1959. Of these tarns Furubergstjärn was without perch and Korsjön did not yield much perch, although both were close to running water and were detached from the big lake. Perhaps easy and free access to a large body of water is important for the overwintering of the perch population and these two tarns did not have such easy and free access.

In the Tärna region (Map, Fig. 7) perch was introduced into Lake Stenträsk in 1925 (information from Mr Fritz Sedholm, in Andersson 1978). Perch then constituted a high proportion of the yield from this small lake, but it has not managed to initiate any substantial population in the adjoining Lakes Votjajaur (at the same altitude), Sejmajaur and Nedre Björkvattnet. Lake Nedre Björkvattnet is a larger lake into which whitefish was introduced in the 1920s. All these Tärna lakes are now combined into one lake reservoir in 1962—63, together with Lake Gardsjön, the Lake Gardiken reservoir, but perch has nowhere formed successful large populations.

Perch in the Tärna region, however, has a rather longer history than perch in Lake Stenträsk. The existence of perch above the crucial water-

Fig. 7. Map of the Tärna lakes before the lake reservoir was constructed.

fall at Forsmark (forming a block to upward migrations) is documented as follows:

1879, F. TRYBOM, reprinted 1977, *cf.* references. Perch in Lake Gardiken.
1896, The Agricultural Board of Sweden. A general inventory of the fisheries.
1913, T. FREIDENFELT. An inventory of the Tärna lakes.
1921, O. OLOFSSON. Notes now mimeographed at the Drottningholm institute. Perch in a small enclosure from Lake Gardiken.
1955, S. RUNNSTRÖM and T. LINDSTRÖM. Report from the meeting with the fishermen held by the institute. Perch was said to keep to small tarns in the vicinity of Lake Vojtjajaure.

The perch introduced into Lake Stenträsk was taken from a small tarn running to the Tärna lake system and thus redistributed only within the Tärna region. Only one of the other sources mentions that perch has been brought by man past the Forsmark waterfall, and the informant in question lived in another district (one of the two informants in OLOFSSON's report of 1921). An introduction of perch above the waterfall is possible but so far has not been documented. Any such introduction must anyhow have taken place long ago, and the perch has failed to expand much from the small tarns and enclosures to larger and more open waters.

There are tarns in this district where perch live without access to larger lakes, probably benefitting from lack of certain other fish species, and there are perch populations on higher altitude (600—700 metres in the southern part of the Swedish high mountains *e.g.* the Rogen district, Fig. 1).

V. PERCH IN THE PELAGIC ZONE

As is stated in several textbooks perch can hunt in the pelagic zone outside the littoral. In the North Swedish inland, however, perch catches in gill nets hung in the pelagic zone seem to be very rare as shown by Table 8. The material comes (1) from Lake Parkijaur in 1970 (*i.e.* the summer immediately preceding the damming of the lake reservoir) and in 1975 — and (2) from Lake Storjuktan in 1967, after five years as a lake reservoir, and (3) from the Lake Håckren reservoir formed from the four Vålå lakes, after 6—7 years as a reservoir.

Echo soundings in the Lake Håckren reservoir in August 1971—73 indicate fish in the shallow regions down to the bottom and over the whole pelagic zone down to 15 metres (Fig. 9; as usual, no data can be obtained in the topmost 2—3 metres). The reservoir fish population is mainly char and perch. In the evenings about sunset fish seem to rise to the surface over the whole lake, out of reach of the echo sounder. There is, however, a small fraction which goes down towards the bottom in the shallow regions. These diving fish may possibly be perch, though the netting does not support this interpretation, but the fish reaching the surface in the evening are probably char according to comparisons with the netting (Table 8).

VI. THE GROWTH OF PERCH ON THE OUTSKIRTS OF ITS DISTRIBUTION

As can be inferred from textbooks *e.g.* WEATHERLEY (1972), growth of perch is not necessarily a simple relation between density of the population and access to appropriate food. An example from perch growth can be found in KJELLBERG (1971). It might be worth while to examine whether growth or average size is poor in the vicinity of the limit of perch distribution. Historical notes from the Tärna district (page 66) suggest that it is. Reports from eight fishermen fishing the perch lakes and tarns in 1953—60 gave a mean weight of 0.151 kg (3,576 perch in all), and a smaller sample from the larger Lake Nedre Björkvattnet gave the mean 0.126 kg (58 perch), the fish being caught by fishermen with access to a well diversified gear set.

Table 9 shows differences between summer data and autumn data on perch mean weight in different mesh sizes from Lakes Parkijaur, Storjuktan and the Vålå lakes. There are interesting differences between the Vålå lakes and the other lakes. Within the Vålå lakes group, lack of catch is common among the coarse-meshed gill nets and Lake Hottön with a poor perch population shows a low mean weight for the three fine-

Table 8. *Catch in pelagic gill nets, suspended over a deep part of the lakes. Lake Parkijaur just before and 5 years after, Lake Storjuktan 5 years after and Lake Hottön six—seven years after the lake reservoir was filled for the first time. Lake Hottön now forms a central part of the Håckren lake reservoir. One gudgeon and one Cottus are not reported in the table below.*

Lake	Date	Fishing depth	Trout	Char	Grayling	Whitefish	Perch	Pike	Burbot
Parkijaur	July 1970	0— 6 m	0	—	0	115	4	0	0
		6—12	0	—	0	124	6	0	0
		12—18	0	—	0	819	1	0	0
		Bottom	0	—	0	469	0	0	15
	September	0— 6 m	0	—	0	433	0	0	0
		6—12	0	—	0	1,838	2	1	0
		12—18	0	—	0	1,537	2	0	0
		Bottom	0	—	0	658	5	0	15
	July 1975	0— 6 m	0	—	0	124	0	0	0
		6—12	0	—	0	198	0	1	0
		12—18	0	—	0	155	0	0	0
		Bottom	0	—	0	274	1	0	1
	September	0— 6 m	0	—	0	86	0	0	0
		6—12	0	—	0	1,279	1	0	0
		12—18	0	—	0	1,323	7	0	0
		Bottom	0	—	0	388	19	1	2
Storjuktan	September 1967	0— 6 m	0	—	0	2,475	0	0	1
		6—12	0	—	0	974	1	0	1
		12—18	1	—	0	323	0	0	0
		18—24	1	—	0	80	0	0	0
Hottön	August 1972	0— 6 m	7	4	0	—	0	0	0
		12—18	0	4	1	—	0	0	0
		24—30	0	0	0	—	0	0	0
		36—42	0	0	0	—	0	0	0
	August 1973	0— 6 m	0	4	0	—	0	0	0
		12—18	0	0	0	—	0	0	0
		24—30	0	1	0	—	1	0	0

Lake Parkijaur. Nine floating gill nets, 20 feet deep, set over 28 metres total depth. Mesh sizes knot to knot: 10, 13, 17, 21, 25, 30, 33, 38 and 50 mm, one net each. They were fished one day and one night at each depth indicated, and searched evening and morning.

Lake Storjuktan. Eight floating gill nets, 20 feet deep, set over a total depth of 36 m. Mesh sizes as for Lake Parkijaur, but not 13 mm. They were fished two days and two nights at each depth indicated and searched twice.

Lake Hottön 1972. Nine floating gill nets, 20 feet deep, set over 65 m total depth. Mesh sizes as for Lake Parkijaur. They were fished one day and one night and searched evening and morning. (Furthermore, two floating survey nets (*vide infra*) fished over both 13 and 20 metres, caught 3 trout, 3 char and only 1 perch.)

Lake Hottön 1973. Two floating "survey" gill nets, 20 feet deep, and the same mesh sizes as 1972, set over 78 metres total depth.

meshed gill nets. So also does Lake Gesten, despite the reported good perch section "Gesten NW". It is possible that these fish were washed down from Lake Hottön (a very short stream connected these lakes) and stayed in Lake Gesten inside the big eddy in the inflow, trapped in the inshore part.

Lake Parkijaur has the highest perch yield and Lake Hottön the lowest, so there is some support in the material for the idea that perch

Table 9. *Mean weight of perch for different mesh sizes. For gill-net material and fishing effort, see Table 2. A dash for mean weight in the table indicates no catch or less than 3 perch per 10 gill-net efforts.*

	Mesh size, knot to knot, millimetres								
Lakes	50.0	37.5	33.3	30.0	25.0	21.4	16.7	Season	Year
Parkijaur	—	280	193	156	122	100	56	July	1970
	593	274	199	160	129	89	168	September	1970
	490	251	213	180	129	95	82	July	1975
	—	270	211	192	126	93	59	September	1975
Parkijaur, mean	515	269	204	172	127	94	91		1970—75
Storjuktan	—	—	191	147	77	69	25	June	1958—61
	—	—	—	146	99	102	30	June	1967
	—	—	168	139	98	74	45	July—early August	1957—61
	—	—	—	161	96	78	56	Late August—Sept.	1958—61
	488	250	237	184	150	121	47	Late August—Sept.	1967
Storjuktan, mean	—	286	191	155	104	89	41		1957—67
The Vålå lakes, mean	—	—	—	110	111	68	42		1957
Aumen	—	—	147	126	108	75	37	June	1957
	—	221	172	118	120	124	57	August	1957
Hottön	—	—	—	—	—	63	30	June—July	1957
	—	—	—	—	193	54	36	August	1957
Gesten	—	—	—	—	—	41	36	June	1957
	—	—	114	112	85	59	49	August	1957
Håckren	—	—	—	98	78	64	44	July	1957
	—	—	—	98	82	62	49	September	1957
The Vålå lakes, mean	—	—	—	122	103	71	50		1958
Aumen	—	188	150	137	111	125	53	June	1958
	—	242	293	169	288	84	61	August	1958
Hottön	—	—	—	—	61	50	34	June	1958
	—	—	—	—	80	55	48	August	1958
Gesten	—	—	216	102	—	56	52	July	1958
	—	—	—	165	58	56	25	August	1958
Håckren	—	—	—	117	90	62	56	July	1958
	—	—	—	106	94	77	67	August	1958

size is small at the margin of the distribution. Under good local circumstances this is not manifest, as in Lake Aumen, section "Skåltjärn" 1958.

Perch growth in the Lake Parkijaur reservoir (1975), Lake Storjuktan (1961) and the Lake Håckren reservoir (1972, 1973) is studied on opercula and perch growth in the Vålå lakes on scales. Comparisons with other perch growth studies in Sweden (Agnedahl 1968, Neuman 1974 c, 1976) suggest that the first year length from the present opercula study may be overestimated. The detection of the first annuli on opercula is known to be crucial. The possibility cannot be excluded that some first year annuli have been overlooked in some specimens and that the figure for first year length should be correspondingly reduced. The results we obtained are presented in Fig. 8. Scales have a known tendency to form false annuli (*cf.* Nilsson 1921), and this is confirmed on material from Lake Hornavan, a deep lake close to the distribution limit of perch, altitude 425 metres. The information obtained by comparing opercula and scales from Lake Hornavan is used when studying the growth of perch in Lakes Hottön and Aumen on scales (Fig. 8).

The growth is good in the studied lakes as shown by a comparison with some other Swedish perch populations, *cf.* Neuman 1974 c.

The growth in the samples is fairly similar and could hardly explain the difference between the Vålå lakes, Lake Parkijaur and Lake Storjuktan in Table 9. Lack of old fish in the Vålå lakes could provide the explanation.

VII. DISCUSSION

A discussion of the factors governing perch distribution can be helpful for a study of their habitat choice. (The lakes in this study are, however, not on the ultimate altitudinal limit of perch in Sweden, see page 66.) In an analysis of the processes governing fish distribution, a formal distinction could be made between two topics:

(1) the appropriate growth and behaviour of adult fish, giving the eggs, larvae and young the necessary prerequisites for a successful passage through the critical periods, and
(2) the way in which environmental factors, including competition and predation, can allow a sufficient number to survive from eggs.

The way in which the two processes interact will not be discussed in this paper.

Starting with the first theme, it is important to discuss how perch migration and growth are influenced by temperature. A well-known author of books in Swedish on fishing and fishery biology Lindhé (1976) begins one chapter by saying that a thermometer is an indispensable part of the equipment of anybody fishing for perch. Seasonal migrations could easily be conceived of as being a response to the temperature cycle.

According to Allen (1935), perch spend the winter in the deep parts of Lake Windermere and move towards the shallow regions in the spring. The indications in the present material on such seasonal migrations have no doubt only a low statistical significance, but they make it appear at least likely that the perch in the North Swedish inland lakes follow the quoted pattern, a pattern also described by Worthington (1949) and Agnedal (1968, Lake Erken, Central Sweden).

Superimposed on the seasonal migration is diel migration such as described by Hasler and Bardach (1949), Eriksson (1974), Thorpe in Percis 1977. Small perch inhabiting very deep regions in great lakes in the summer (Andersson 1942 and other textbooks) could represent a further development of the pattern; such perch is suspected to be a divergent fraction, though not genetically isolated from the bulk of the population. In the Baltic, an environment diverging from the inland lakes, perch change their habitat from the shore-near, limnetic parts which they inhabit in the spring to include also deeper parts in late summer and autumn. This is interpreted as an indication that temperature is a factor governing the habitat segregation between limnetic and marine species (Neuman 1974 b, 1979 b), high temperatures favouring the limnetic species. The material does not cover the midwinter situation.

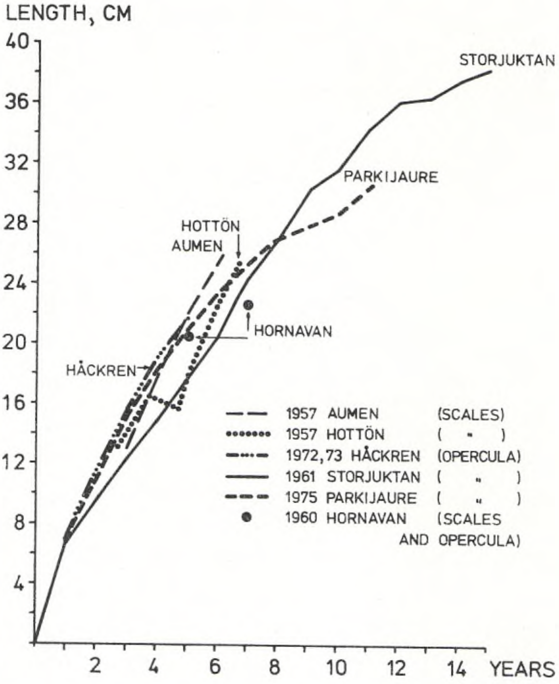

Fig. 8 Growth of perch.

A good deal is known about the preferred temperature and temperature selection in fish. In particular, it has been established:

(1) that there is a seasonal variation in preferred temperature (Sullivan and Fisher 1953, Fry 1971, p. 80, Neuman 1974 a, 1979 b, — a circumstance relevant for a correct understanding of the main seasonal trend in the migrations — and (2) that there are variations within species in temperature selection that have not been fully explained (Fry 1971, pp. 79 ff.) — relevant for an understanding of the divergent fraction.

On looking a little further into variation in migration pattern, we find that perch can also inhabit the pelagic part of great lakes, whether this occurs sporadically in an oligotrophic lake (Lake Bolmen, southern part, Southern Sweden: Hamrin 1976), or in eutrophicated great lakes

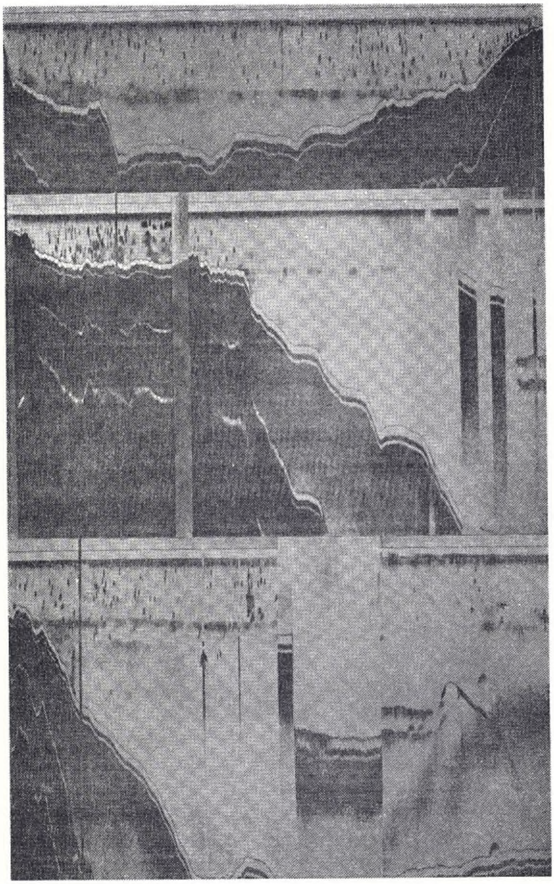

Fig. 9. Echo sounding from the lake reservoir Håckren, August 22—23, 1972. A shallow section with char in the upper parts of the pelagial and on the banks, close to the shore, 5.30—6 p.m. In the centre a deeper section, 7.15—7.45 p.m. Sunset occurred as the sounding was extended out in the pelagial, and the char rose to the surface, out of range for the echo sounder. Below: the same section, 3—3.30 a.m., with some char echoes reappearing in the upper parts of the pelagial.

(Lake Geneva: Grivaz 1948, Tesch 1955; Lake Mälaren: Northcote and Rundberg 1970) or in a very different environment, Northern Norway close to sea level (Klemetsen 1973). Such pelagic occurrence is not known from the North Swedish inland lakes here studied (Table 8, Fig. 9). It is difficult to provide a simple explanation of these migrations out into the pelagic part (when they occur). It is probable that food is often changed when perch shifts its habitat (Klemetsen, *op.cit.*); search for food may be the basic reason for the migration or the food composition may be a mere consequence of the migration. Diel movements in the pelagic were actually upward in the nights in July in Lake Mälaren.

One partial explanation for differences between lakes in migration pattern could be hazarded: differences of species composition between lakes. In North Norway there is only pike and perch, in the North Swedish lakes char or whitefish dominates and other species are tabulated in Table 1, in Lake Mälaren there are vendace, pike, smelt, perch and roach and seven minor poulations including threespined stickleback and pikeperch. In the Norwegian case, for instance, lack of the two dominating species in the North Swedish lakes, whitefish and char, may make it easier for perch to enter the pelagic part, but on the other hand there are no whitefish young as food that could make it rewarding to do so. Whitefish young occur pelagically in North Swedish whitefish lakes like Parkijaur and Storjuktan but perch does not (Table 8).

To conclude this discussion on variation in seasonal migration pattern, such migrations out into the pelagic part occur only at high water temperature, and so temperature is involved as it was in the probable control of the seasonal migration between deep and shallow water, the migration relevant to the present material.

The discussion of this migration between deep and shallow water and the habitat choice of perch on the outskirts of its distribution area will very largely be concerned with the best strategy when perch is expending the resources of energy that the fish has acquired through feeding. The paramount importance of temperature for this strategy has been shown by Fry (*e.g.* 1971) and Brett (1971, 1973). A case has been worked out for perch in the Baltic by Neuman (1974 a, c, 1976, 1979 b) and the present discussion will follow their presentation in essential parts. Where a species inhabits the northern border area or the altitudinal border area of its distribution range, the influence of temperature on the strategy of the population should, however, be particularly important. As a first approach it will be examined whether much of the habitat choice and the growth picture can be explained mainly by reference to the effects of this single factor.

The choice of winter habitat at a certain depth below the surface is influenced by the need of a warm-water species to economize its energy resources in cold water (*e.g.* VARLEY 1967, CHRISTIE and REGIER 1973, MCLEOD quoted by CHRISTIE and REGIER). Part of the available resources will then be used up for the migration to the spring and early summer habitats. These habitats in the Vålå and Tärna districts are bays and detached, rather small waters with free access to the main body of the lakes and are traversed or fed by minor tributaries. The choice of these peripheral habitats is probably governed by a search for high temperature at that season. The peripheral waters will be heated most rapidly during spring and early summer. The minor tributaries do not have deep and cool lakes in their precipitation areas, and the vegetation is often well developed in their mouth areas and in the adjacent peripheral waters. Thus there were, *e.g.*, *Carex* reeds in Skåltjärn, *Potamogeton* and *Myriophyllum* in other places, etc. This macrovegetation may embrace isolated water masses in the detached waters with slow water exchange with the main lakes. The open shores of these lakes close to the high mountains are otherwise very poor in macrovegetation apart from *Isoëtes* and other isoëtides. (There is a comprehensive study of the vegetation by MELLQUIST *et al.* 1955—57.) The higher temperature that is built up during calm days on these open shores falls rapidly again on windy days, so they may be less suitable on the outskirts of the perch distribution.

Even in the most rapidly heated peripheral waters under the protection of the macrovegetation, the preferred temperature will not be attained very soon: however, it is not easy to apply laboratory preferenda observations to field situations (NEUMAN 1974 a). The activity available within the "scope" for activity that the perch after all do manage to obtain in the peripheral waters has to be divided between spawning and restoration of the condition of the adults after spawning.

Additional expenditure of activity could furthermore occur in the running water of the small tributaries, but this can be avoided in the habitats observed.

In lakes in Northern Sweden situated a little less close to the distribution limit, perch is known to occur very close to the shore on hot summer days. It is termed "bathing perch" ("*badabborre*"), and it causes trouble to fishermen netting for the whitefish in, *e.g.*, the Lakes Storavan-Uddjaur, altitude 420 metres. In Lake Storjuktan at a slightly lower altitude (but still about 100 metres above Lake Parkijaur), more perch were caught in those sections that resembled the perch habitats in the Vålå and Tärna lakes. From these observations it can be inferred that temperature is important for the choice of summer habitat in the Arjeplog lakes and Lake Storjuktan too.

The activity available within the "scope" for activity in the warmest part of the lakes has to be utilized after the spawning for the restoration of the condition of the adults. Thereafter, growth will follow, provided this is possible before the lakes have cooled again. The use of the resources for growth during a year cycle should be delicately attuned in order to give best performance for adults and optimal preconditions for eggs, the quality of eggs being influenced by the state of the females. It is not *a priori* evident that a good growth is imperative for the best strategy on the outskirts of the distribution area, so information from the studied cases should give a necessary foundation.

The average size of perch in the material studied is small in the Vålå and Tärna lakes. The fishing for perch is at least in the Vålå lakes and in the Tärna lakes outside the perch tarns very unimportant, so poor growth and high natural mortality remain as explanations for the small size. Occasionally better-sized perch occur (Skåltjärn in 1958). Variation in population size seems to occur sometimes too, as is indicated by catches reported by BRUNDIN (1942) from Lake Hottön. Variation, sometimes extreme, in recruitment, natural mortality and population size is rather to be expected in a lake at the limit of the distribution area, where the environment is likely to be very unfavourable in certain years when it is difficult to meet the demands placed on the energy budget. No indications on poor growth have been obtained so far.

If other explanations of the small perch size than the constraints imposed by the energy

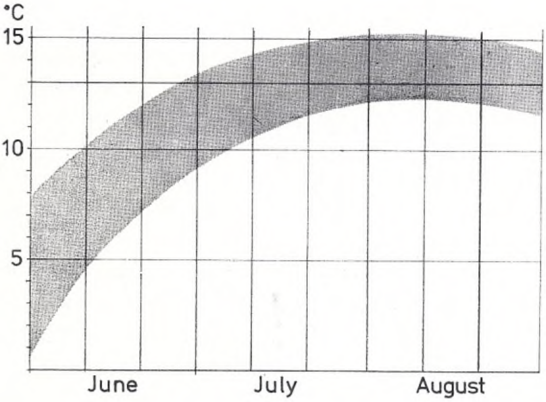

Fig. 10. Summer temperatures in Lakes Parkijaure, Storjuktan, the Tärna lakes and the Vålå lakes and the corresponding reservoirs. The graph is constructed from observations, mainly unpublished, made in connection with survey netting, plankton sampling or whitefish fry studies. A few observations from very cold or very warm summers fall outside the fan-shaped figure.

budget are sought, the effect of the fish fauna composition could be suspected to be important for the perch growth. Most of the sampled perch are of a size at which according to other studies they ought to feed on fish (Agnedal 1968; *cf.*, however, Sumari 1971). The access to small whitefish as food in Lakes Storjuktan and Parkijaur as compared with the Vålå lakes without whitefish, is not reflected in the size of perch in the three smallest-meshed nets, but rather in the absence of catch in the coarse-meshed nets in the Vålå lakes. A perch of just over 1 hg is on the borderline between perch caught in fine-meshed nets and perch caught in coarse-meshed nets. A perch of this size might have some difficulty in catching one-year-old whitefish, which measure more than 10 cm. The perch size class in question could rather be expected to take mainly young-of-the-year whitefish, if any whitefish at all. Up to this crucial perch size there is no great difference in perch growth between Lakes Parkijaur and Storjuktan and the Vålå lakes. The growth is rather good as could be seen by a comparison with other Swedish perch populations, *e.g.* Neuman 1974 c, 1976. Above that size, the catch of perch in the Vålå lakes is generally very small; so lack of appropriate food and again, higher natural mortality in the Vålå lakes provides the most likely explanation of the small size.

The second topic proposed at the beginning of the discussion concerned the survival of eggs and young in the habitat chosen as spawning area by the parents. The temperatures observed in the shore region of the Tärna and Vålå lakes and Lake Storjuktan (fishing surveys and plankton studies) can sometimes be very low in spring and early summer, when strong winds exert an equalizing influence on the lake water. The temperature has, however, passed the 3—5° level, shown to be critical for perch embryos (Hokanson and Kleiner 1974, Swift 1965), and at the beginning of June has reached the range 6—7° which is indicated by these authors to be the lower TL 50 for total hatching of *Perca fluviatilis*. The range 6—7° is also lower TL 50 for normal hatching of *Perca flavescens* and the lower limit for normal hatching (not premature). On the other hand, the 13°C level, *i.e.* the lower limit for the optimal range of swim-up larvae, is sometimes not reached until August (Fig. 10). (*P. flavescens* is suspected by Hokanson and Kleiner (1974) to be conspecific with *P. fluviatilis* on the basis of the very similar results of temperature experiments with those two species.)

The experiments reported were performed at constant temperatures. When rising temperatures were used (range 4.9—24.3°C), the survival and hatching results improved. Furthermore, the temperatures from the lakes in the present study were not read in the shallow peripheral waters and reed belts that are the typical habitat of the adults in spawning time, *i.e.* the habitat for eggs and young, where the temperatures should be higher than along the open shores. In many other lakes in Northern Sweden, perch young are regularly observed in the macrovegetation close to the shore inside the *Phragmites* reed belt, where such exists. The preferred temperature of young perch has been shown to be higher than that of adults (Ferguson 1958). All these facts support the idea that the habitat choice of adult perch in spring and early summer is in the long run also governed by the conditions for successful hatching and survival of eggs and young.

So far, the temperature effects on the habitat choice of adult perch and on the survival of the young have been touched on. If any one factor is to be considered of paramount importance, it is temperature. No doubt, a large number of other factors are important too. The outcome in habitat choice, etc., is a response to a multifactorial and very complicated environment.

VIII. NOTES ON PERCH POPULATIONS IN LAKE RESERVOIRS

Most of the perch caught in this study were of the size where they should have turned to fish prey, the final food choice in their life cycle (Agnedal 1968, Percis 1977; there are exceptions in extreme environments, such as perch in acid lakes, Andersson 1972, or perch in the northern part of Norway, Klemetsen 1973). Many of the perch sampled for this study were born before the transformation of Lakes Parkijaur and Storjuktan into reservoirs, as the reservoirs were five years old when the last fishing was performed. The Lake Håckren reservoir was fished for the last time six and seven years after the reservoir was built. The ecological upheaval that started when the lakes were transformed had not quite subsided 5—7 years later.

One has to consider the reaction of some pre-reservoir and some post-reservoir year classes in an environment where (1) the "damming up" effects on the food animal population had not yet ceased (Grimås 1965, 1970, Nilsson 1964, 1973, Lindström 1973) and (2) the whitefish of a small-sized species had increased on the bottom at a certain depth in Lake Storjuktan (Lindström and Filipsson 1972) and (3) a small-sized whitefish species occupied deep parts of Lake Parkijaur along the bottom (no increase or decrease has so far been ascertained, Bergstrand 1977).

One should not, however, place too much emphasis on the changes in food animals for halfgrown and adult perch in lake reservoirs at high altitude. The access to peripheral waters with good temperature conditions is the most important habitat prerequisite that emerges from this study. Long-term trends in recruitment of perch populations in lake reservoirs at high altitudes should thus depend, *inter alia* on the creation of similar habitats along the new shores in the inundated terrain. In reservoirs with high amplitude, the shore may differ very much from one year to another depending on the filling of the reservoir. If spawning occurs, the substrate must be dead branches and roots flushed by the rising water. Peripheral waters in reservoirs have a very stony bottom. Food for young perch should mainly consist of plankton developed there during the spring and early summer — perch fry were never caught in the plankton samples in the pelagic parts of the Vålå lakes — unless the peripheral waters are fed by small tributaries. If so, the conditions may remain less changed from the original state. Judging from what we have seen of reservoirs in Sweden, the occurrence of appropriate habitats for perch reproduction in lake reservoirs at high altitudes and with high amplitude are not as frequent as in normal lakes in this district.

Char and perch interact (*cf.* Filipsson and Svärdson 1976, Svärdson 1976), and the increase in char catches in the Lake Håckren reservoir during its first years (Öhman 1969) could be an indication on a new pattern in the interaction. The increased catches were based on pre-reservoir char year classes.

Special attention should be given to the occurrence of perch in deep regions of the Lake Håckren and Storjuktan reservoirs (p. 59, 60). Densities of invertebrate food animals increase substantially somewhere below the draw-down limit (Grimås 1965, 1970). A concentration of small-sized whitefish species within a depth around 15—25 metres has been traced by echosounding in some reservoirs (Lindström 1967), and this concentration of potential prey fish touches the corresponding depth curves of the lake bottom, where the perch stay. At present it is not possible to make even a crude estimate as to what proportion of the total population is constituted by such deeply occurring perch.

A hypothesis for the development of perch populations in lake reservoirs on the outskirts of their distribution should be based *inter alia* on decreased recruitment due to lack of suitable spawning areas, decreased natural mortality due to decrease in the trout populations and a deeper occurrence of adult perch.

IX. SUMMARY

The vertical and horizontal distribution of perch was studied in some Swedish lakes and lake reservoirs by means of catches in bottom nets, set at different depths and stations, and in pelagic nets and with the aid of echo sounding. Growth was also studied. Some waters lay near the distribution limit, others lay further downstream. The migration and growth of the perch are interpreted in terms of the best strategy when the fish is expending the energy it has acquired. Close to the border area of its distribution, the influence of temperature on this strategy is particularly important. So the summer habitat in the lakes close to the high mountains consists of rapidly heated bays and detached, rather small waters with free access to the main body of the lakes and traversed or fed by minor tributaries.

Growth is rather good. A marked variation in recruitment and natural mortality is indicated for lakes on the outskirts of the distribution. When small whitefish is not available as food, perch above 1 hg tends to be rare, probably owing to higher natural mortality.

A hypothesis for the development of perch populations in lake reservoirs on the outskirts of its distribution is based on the following assumptions: decreased recruitment due to lack of suitable spawning areas, decreased natural mortality due to decrease in the trout populations and a deeper occurrence of adult perch.

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Bottom Fauna of Small Acid Forest Lakes

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CONTENTS

I. INTRODUCTION

The increased acidification of lakes and rivers in Scandinavia and certain parts of Canada must be considered one of the most acute environmental problems in those parts of the world today. Several studies of the causes and consequences of the acidification have been published during the last ten years (BRAEKKE 1976, SCHOFIELD 1976, ALMER *et al.* 1978).

The available knowledge of the effects on water chemistry (DICKSON 1975, ALMER *et al.* 1978), algae, higher vegetation and mosses (GRAHN *et al.* 1974, LEIVESTAD *et al.* 1976, ALMER *et al.* 1978) and especially fish (HULTBERG 1975, MILBRINK and JOHANSSON 1975, LEIVESTAD *et al.* 1976, ALMER *et al.* 1978) is relatively good. Studies concerning the effects on zooplankton and macrobenthos are less numerous.

HARRISON (1958) and PARSON (1968) investigated the effects of acid effluents on the biology of running waters.

In Norway, it has been shown that certain groups of animals (Gastropoda, *Gammarus lacustris* and *Lepidurus arcticus*) (J. ØKLAND 1969, K. A. ØKLAND 1969, BORGSTRÖM and HENDREY 1976) are never found in waters with pH-values near 5 or even 6. Moreover, the number of species of Ephemeroptera and Plecoptera decreases rapidly with decreasing pH-value (LEIVESTAD *et al.* 1976).

GRAHN *et al.* (1974) pointed out that the number of species was lowest in the most acid of the six lakes studied and that the greater part of the bottom fauna in these lakes consisted of Trichoptera, Odonata, Hemiptera and Megaloptera. According to WIEDERHOLM and ERIKSSON (1977), the composition and depth distribution of bottom animals in the acidified Lake Trestickeln was rather similar to what BRUNDIN (1949) found in the polyhumic Lake Skärshultsjön. However, *Asellus aquaticus* and molluscs were absent in Lake Trestickeln.

In the present paper, the benthic communities of seven small acid forest lakes, with varying pH and water colour, are studied. The investigation was carried out as part of a project at the Institute of Freshwater Research dealing with the application of lime to acidified seepage lakes.

II. LAKE CHARACTERISTICS

The lakes studied are all situated in areas with bedrocks consisting of granites, gneisses and leptites. Lake Trehörningen is located about 20 km south-east and Lakes Svartsjön and Långsjön about 20 km south of Stockholm. Lake Trehörningen is a seepage lake of the River Åvaån system; the other lakes drain into Lake Ådran and then further into Lake Orlången. Lake Trollkarlen is situated in the southern part of the Kilsbergen mountain region some 200 km west-south-west of Stockholm and drains into the River Svartån. Lakes Blanksjön, Iglafallssjön and Vibollsjön all belong to the same water system and drain into Lake Vättern about 200 km south-west of Stockholm.

The more important lake characteristics are shown in Table 1. The lakes studied are small

Table 1. *More important lake characteristics.*

	Height above sea level (m)	Drainage area (ha)	Surface area (ha)	Max. depth (m)
L. Trehörningen	52	75	3.4	4.5
L. Svartsjön	79	11	1.6	7.0
L. Långsjön	79	75	8.0	11.0
L. Trollkarlen	225	13	3.1	11.0
L. Blanksjön	221	60	11.5	15.0
L. Iglafallssjön	168	180	6.1	14.0
L. Vibollsjön	156	440	10.0	7.0

	pH mean (range)	Spec. cond (mS/m)	Colour (mg Pt/l)	Tot.-N [4] (mg/l)	Tot.-P [4] (mg/l)
L. Trehörningen [1]	5.0 (4.2—5.4)	4.3	45	0.35	0.006
L. Svartsjön [1]	4.5 (3.6—4.7)	3.2	30	0.33	0.007
L. Långsjön [1]	4.5 (4.1—4.7)	3.6	70	0.38	0.008
L. Trollkarlen [2]	4.2 (3.8—4.4)	3.7	5	—	—
L. Blanksjön [3]	4.9 (4.0—5.4)	3.0	30	0.56	0.004
L. Iglafallssjön [3]	4.9 (4.3—5.0)	3.1	45	0.52	0.005
L. Vibollsjön [3]	4.7 (4.4—4.9)	3.1	65	0.47	0.006

[1] Mean value of 11 measurements June 1976—June 1977.
[2] Mean value of 4 measurements June 1977—June 1978.
[3] Mean value of 8 measurements June 1977—Aug. 1978.
[4] Mean value of 2 measurements during spring and autumn turnover.

(All values refer to surface-water samples.)

(1.6—11.5 hectares) and acid (pH: 4.2—5.0) and have low concentrations of plant nutrients. As can be seen in Fig. 1, the pH can be very low, especially during early spring.

At the time of bottom fauna sampling, there was no reproducing fish population in any lake. Lake Trehörningen contained a few slow-growing pikes (*Esox lucius*); Lakes Svartsjön and Långsjön contained a population of old perch (*Perca fluviatilis*), which, however, was totally eliminated during the spring flood of 1977. The other lakes had been empty of fish for at least 10 years.

III. MATERIAL AND METHODS

Samples of the bottom fauna were taken with an Ekman grab on April 4, 1977, in Lakes Trehörningen, Svartsjön and Långsjön and on December 12, 1977, and April 14, 1978, in other lakes. Two samples were taken at the depth of 1 and 2 metres respectively and thereafter every other metre to the greatest depth of each lake. The material was sieved through a 0.6 mm net and preserved in formalin. Additional qualitative samples were taken from the shore with a fine-meshed dip net in May 1977 and 1978.

IV. RESULTS AND DISCUSSION

The composition of the benthic communities in the lakes studied can be seen in Tables 2—5. The results show that the main taxa Hirudinea, Ephemeroptera and Mollusca are heavily reduced in acid lakes. The most tolerant species of Hirudinea seems to be *Erpobdella octoculata* and that of Ephemeroptera to be *Leptophlebia vespertina*. The last-mentioned species has in Norway been found in waters with a pH of 4.1 (Hendrey and Wright 1977) and in the present material this species is absent in the most acid lake (pH: 4.2). *Pisidium sp.* (Mollusca) has been found in only two of the lakes and gastropods are totally absent. These findings are also in good agreement with earlier results (J. Økland 1969, *op.cit.*).

Table 2. *Numbers of benthos in Lakes Trollkarlen and Svartsjön (numbers/m²).*

Depth, m	Trollkarlen Dec. 4, 1977						April 14, 1978						shore sample	Svartsjön April 4, 1977				shore sample
	1	2	4	6	8	10	1	2	4	6	8	10		1	2	4	6	
Oligochaeta	—	—	—	—	—	—	—	—	—	—	—	—	+	20	—	20	—	—
Crustacea																		
Asellus aquaticus L.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	60	1260	—	+
Ephemeroptera																		
Leptophlebia vespertina L.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	—	+
Odonata																		
Enallagma cyathigerum CHARP.	—	—	—	20	20	—	—	—	—	—	—	—	+	—	—	—	—	—
Aeshna grandis L.	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—
Cordulia aenea L.	—	20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Leucorrhinia dubia LINDEN	—	—	—	—	—	—	—	20	—	—	—	—	+	—	—	—	—	+
Sympetrum flaveolum L.	—	—	—	—	—	—	—	—	—	—	—	—	—	80	20	20	—	+
Megaloptera																		
Sialis lutaria L.	200	20	100	60	20	20	120	—	40	20	—	—	+	20	60	40	—	+
Heteroptera																		
Corixa sp.	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—
Notonecta glauca L.	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—
Trichoptera																		
Agrypnia varia FBR.	—	—	—	—	—	—	—	—	—	—	—	—	+	20	—	—	—	—
Cyrnus flavidus McL.	—	—	—	—	—	—	—	—	—	—	—	—	+	40	40	120	—	+
Holocentropus dubius RAMB.	—	—	—	20	—	—	—	20	—	—	—	—	+	20	—	60	—	+
Coleoptera																		
Dytiscus lapponicus GYLL.	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—
Rhantus exsoletus FORST.	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—
Araneida																		
Argyroneta aquatica CLERK	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—
Diptera																		
Ceratopogonidae	40	—	100	40	40	20	—	80	—	—	—	—	—	—	—	—	—	—
Chaoborus flavicans MEIG.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	40	—
C. obscuripes v. d. W.																		
Ablabesmyia sp.	—	20	40	80	40	80	—	180	—	—	220	20	+	240	20	220	—	+
Clinotanypus nervosus MEIG.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	—	—	—
Procladius sp.	40	20	—	—	—	80	60	20	20	—	20	40	+	160	40	20	80	—
Heterotrissocladius marcidus WALK.	20	—	20	—	40	—	—	—	—	—	—	—	—	—	—	—	—	—
Psectrocladius sp.	—	200	100	200	280	60	—	80	20	—	300	40	—	20	20	100	—	+
Zalutschia potamophilus CHERN.	—	—	—	—	—	—	—	—	—	—	—	—	—	20	—	—	—	—
Chironomus anthracinus-gr.	2120	2260	80	600	—	560	3460	1380	60	100	—	880	—	60	200	180	220	—
C. plumosus-gr.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	40	—	+
C. tentans FBR.	—	—	—	—	—	—	—	—	—	—	—	—	—	160	—	—	—	—
C. thummi-gr.	—	—	—	—	—	—	—	—	—	—	—	—	—	120	—	—	—	—
Limnochironomus sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	20	20	—	—	—
Pagastiella orophila EDW.	—	—	—	—	—	—	—	—	—	—	—	—	—	20	60	40	—	—
Phaenopsectra longiventris K.	—	—	—	—	—	120	—	—	20	—	—	180	—	—	—	80	—	—
Tanytarsus sp.	—	—	—	—	60	20	—	20	—	—	—	—	—	—	—	—	—	—
Total	2420	2540	440	820	500	960	3640	1800	160	120	540	1160	—	1020	540	2220	340	—

Table 3. *Numbers of benthos in Lakes Långsjön and Vibollsjön (numbers/m²).*

Depth, m	Långsjön April 4, 1977						shore sample	Vibollsjön Dec. 3, 1977					April 14, 1978				shore sample
	1	2	4	6	8	10		1	2	4	6	8	1	2	4	6	
Oligochaeta	60	—	—	20	—	—	+	280	20	—	—	—	640	—	—	—	—
Crustacea																	
Asellus aquaticus L.	20	—	—	—	—	—	—	940	320	200	—	—	200	1100	—	—	—
Ephemeroptera																	
Leptophlebia vespertina L.	—	—	—	—	—	—	+	320	—	20	—	—	180	60	—	—	—
Odonata																	
Enallagma cyathigerum Charp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Cordulia aenea L.	—	—	—	—	—	—	—	60	—	—	—	—	—	—	—	—	—
Sympetrum flaveolum L.	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—
Megaloptera																	
Sialis lutaria L.	80	60	—	—	—	—	+	60	—	—	—	—	120	20	—	—	—
Heteroptera																	
Corixa sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Cymatia bonsdorffi Sahlb.	—	—	—	—	—	—	—	20	—	—	—	—	20	—	—	—	—
Notonecta glauca L.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Trichoptera																	
Agrypnia obsoleta McL.	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—
A. varia Fbr.	—	—	—	—	—	—	—	—	—	—	—	—	40	—	—	—	—
Cyrnus flavidus McL.	20	40	—	—	—	—	—	20	20	20	—	—	80	—	—	40	—
Holocentropus dubius Ramb.	—	—	—	—	—	—	—	20	—	—	—	—	20	—	—	—	—
Lamellibranchia																	
Pisidium sp.	—	20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Diptera																	
Chaoborus flavicans Meig.	—	—	—	—	—	8040	—	—	—	—	80	5120	—	—	—	—	—
C. obscuripes v. d. W.	—	—	—	—	—	—	—	—	20	—	—	—	40	20	—	—	+
Ablabesmyia sp.	—	—	—	—	—	—	+	700	100	—	—	—	380	20	—	—	—
Procladius sp.	380	40	120	140	80	—	—	120	80	20	—	—	20	100	40	—	—
Heterotrissocladius marcidus Walk.	—	—	20	—	—	—	—	—	—	—	—	—	80	—	—	—	—
Psectrocladius sp.	—	—	—	—	20	—	+	20	—	—	—	—	—	—	—	—	+
Zalutschia zalutschicola Lip.	—	60	3220	160	80	—	—	—	—	—	—	—	—	—	—	—	—
Chironomus anthracinus-gr.	420	160	—	—	—	—	—	80	140	—	—	—	120	20	300	—	—
C. plumosus-gr.	—	—	—	—	—	—	+	—	—	580	120	100	—	—	260	—	—
C. tentans Fbr.	200	—	—	—	—	—	—	—	—	—	40	—	140	—	—	—	—
C. thummi-gr.	—	—	—	—	—	—	—	—	—	100	40	—	—	—	—	—	—
Cryptochironomus sp.																	
Endochironomus dispar-gr	—	—	—	—	—	—	—	—	40	—	—	—	—	—	—	—	+
Limnochironomus sp.	20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pagastiella orophila Edw.	40	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Phaenopsectra longiventris K.	—	—	180	500	1140	80	—	—	—	60	20	—	—	—	—	—	—
Tanytarsus sp.	—	—	—	—	—	—	—	—	—	—	40	—	—	—	—	—	—
Total	1240	380	3540	820	1320	8120	—	2640	740	1000	340	5220	2080	1340	600	40	—

Table 4. *Numbers of benthos in Lake Blanksjon (numbers/m^2).*

Depth, m	Dec., 3, 1977								April 14, 1978							shore sample
	1	2	4	6	8	10	12	14	1	2	4	6	8	10	14	
Oligochaeta	380	20	—	60	—	—	—	—	20	—	—	60	—	—	—	+
Hirudinea																
Erpobdella octoculata L.	—	—	—	—	—	—	—	—	—	20	—	—	—	—	—	+
Crustacea																
Asellus aquaticus L.	920	540	380	40	—	20	40	—	1940	340	40	80	140	40	—	+
Ephemeroptera																
Leptophlebia vespertina L.	—	60	—	—	—	—	—	—	160	60	—	—	—	—	—	+
Odonata																
Enallagma cyathigerum CHARP.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Aeshna grandis L.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Cordulia aenea L.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Leucorrhinia dubia LINDEN	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Sympetrum sp.	—	—	—	—	—	—	—	—	100	—	—	—	—	—	—	—
Megaloptera																
Sialis lutaria L.	140	40	40	40	20	80	40	20	—	100	20	—	—	20	—	—
Heteroptera																
Corixa sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Notonecta glauca L.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Trichoptera																
Agrypnia obsoleta McL.	60	—	—	—	—	—	—	—	60	40	—	—	—	—	—	+
A. varia FBR.	20	—	—	—	—	—	—	—	60	—	—	—	—	—	—	—
Cyrnus flavidus McL.	—	—	—	—	—	—	—	—	60	40	—	—	—	—	—	—
Holocentropus dubius RAMB.	—	—	—	—	—	—	—	—	120	20	—	—	—	—	—	—
Limnophilus sp.	20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Araneida																
Argyroneta aquatica CLERK	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Diptera																
Chaoborus flavicans MEIG.	—	—	—	100	160	240	120	280	—	—	—	—	—	—	900	—
C. obscuripes v.d.W.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Ablabesmyia sp.	120	140	220	—	—	—	—	20	240	40	40	—	—	—	—	+
Macropelopia sp.	—	—	—	—	—	—	—	—	—	—	—	20	—	—	—	—
Procladius sp.	320	300	60	—	—	40	40	20	—	360	80	120	—	—	20	—
Psectrocladius sp.	—	1580	160	60	20	—	—	40	20	20	20	—	—	—	—	—
Chironomus anthracinus-gr.	420	180	100	100	20	—	—	—	20	1160	20	200	20	—	—	—
Cryptochironomus sp.	—	—	20	—	—	—	—	—	—	—	—	—	—	—	—	—
Endochironomus dispar-gr.	60	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Limnochironomus sp.	20	80	—	—	—	—	—	—	80	—	—	—	—	—	—	—
Pagastiella orophila EDW.	20	1040	180	40	—	—	—	—	—	140	—	—	—	—	—	—
Phaenopsectra longiventris K. STAEG.	100	—	20	100	360	620	420	680	—	20	20	160	400	560	—	—
Pseudochironomus prasinatus	—	60	—	—	—	—	—	—	20	40	—	—	—	—	—	—
Tanytarsus sp.	120	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	2720	4040	1200	540	580	1000	660	1060	2900	2400	240	640	560	620	920	—

Table 5. *Numbers of benthos in Lakes Iglafallsjön and Trehörningen (numbers/m²)*

Depth, m	Iglafallsjön Dec. 3, 1977						April 14, 1978							shore sample	Trehörningen			shore sample
	1	2	4	6	8	10	1	2	4	6	8	10	14		1	2	4	
Turbellaria																		
Dendrocoelum lacteum O.F.M.	—	—	—	—	—	—	20	—	—	—	—	—	—	—	20	80	—	—
Oligochaeta	260	—	—	—	—	—	1120	—	—	—	—	20	—	+	40	420	—	+
Crustacea																		
Asellus aquaticus L.	380	20	80	40	—	—	1480	320	40	—	—	—	—	+	20	2720	—	+
Ephemeroptera																		
Leptophlebia vespertina L.	—	120	—	—	—	—	40	—	—	—	—	—	—	+	—	—	—	+
Odonata																		
Enallagma cyathigerum Charp.	—	60	—	—	—	—	—	—	—	—	—	—	—	+	—	20	—	+
Coenagrion sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	20	—	—
Aeshna grandis L.	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	+
Cordulia aenea L.	40	—	—	—	—	—	60	—	—	—	—	—	—	—	—	—	—	+
Leucorrhinia dubia Linden	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Sympetrum flaveolum L.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Megaloptera																		
Sialis lutaria L.	40	140	40	60	20	20	40	40	40	20	40	—	—	+	20	—	—	+
Heteroptera																		
Corixa sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	+
Cymatia bonsdorffi Sahlb.	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	+
Notonecta glauca L.	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—
Trichoptera																		
Agrypnia obsoleta McL.	20	—	—	—	—	—	60	40	—	—	—	—	—	+	—	—	—	—
Cyrnus flavidus McL.	20	—	—	20	—	—	—	20	—	—	—	—	—	+	20	—	—	+
Holocentropus dubius Ramb.	160	—	—	—	—	—	—	—	—	—	—	—	—	+	60	60	—	+
Limnophilus sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—
Nemotaulius punctatolineatus Retz.	—	—	—	—	—	—	20	—	—	—	—	—	—	—	—	—	—	—
Phryganea bipunctata Retz.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	—	—	—
Coleoptera																		
Dytiscidae non det.	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—
Gyrinus sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—

Table 5. Continued.

Depth, m	Iglafallsjön Dec. 3, 1977						April 14, 1978							shore sample	Trehörningen			shore sample
	1	2	4	6	8	10	1	2	4	6	8	10	14		1	2	4	
Lamellibranchia																		
Pisidium sp.	—	—	—	—	—	—	—	20	40	—	—	—	—	—	—	—	—	—
Diptera																		
Ceratopogonidae	—	—	—	—	—	—	40	—	—	—	—	—	—	—	—	—	—	+
Chaoborus flavicans MEIG.	—	—	—	20	80	180	—	—	—	—	—	20	2140	—	—	—	600	—
C. obscuripes v.d.W.	—	20	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	+
Ablabesmyia sp.	260	—	40	—	—	—	80	100	—	—	—	20	—	+	40	220	—	+
Macropelopia sp.	—	—	—	—	40	—	—	—	—	—	—	40	—	—	—	—	—	—
Procladius sp.	180	680	120	40	20	60	40	260	—	100	80	20	—	—	—	—	—	—
Heterotrissocladius marcidus WALK.	—	—	20	20	—	—	—	220	180	—	—	—	—	—	—	—	—	—
Psectrocladius sp.	20	20	20	—	—	—	—	100	60	—	—	—	—	—	40	40	—	+
Zalutschia potamophilus CHERN.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	240	—	—
Chironomus anthracinus-gr.	—	2260	520	180	20	40	—	660	480	260	40	20	—	—	20	—	5480	—
C. plumosus-gr.																		
Cryptochironomus sp.	—	—	—	—	—	—	—	20	—	—	—	—	—	—	—	—	—	+
Endochironomus dispar-gr.	—	—	—	—	—	—	20	—	20	—	—	—	—	—	—	—	—	+
Lenzia sp.	—	—	—	—	—	—	—	20	—	—	—	—	—	—	—	—	—	—
Limnochironomus sp.	20	40	40	—	—	—	—	80	—	—	—	—	—	—	—	—	—	—
Pagastiella orophila EDW.	60	2320	20	—	—	—	—	680	80	—	—	—	—	—	40	—	—	—
Phaenopsectra longiventris K.	—	—	20	1320	300	940	—	—	40	900	860	3700	—	—	—	—	—	—
Polypedilum convictum-gr.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	60	—	—	—
P. nubeculosum-gr.	20	—	—	—	—	—	—	—	20	—	—	—	—	—	—	—	—	—
Pseudochironomus prasinatus STAEG.	—	60	40	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tanytarsus sp.	—	—	—	—	—	—	20	—	—	—	—	—	—	—	—	—	—	—
Total	1480	5740	960	1700	480	1240	3040	2640	1000	1280	1020	3840	2140	—	440	3820	6080	—

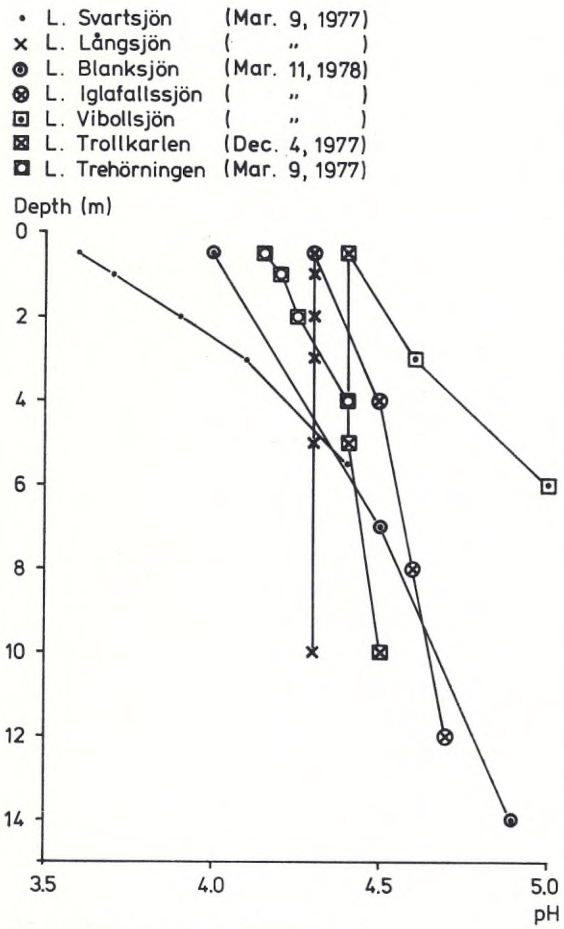

Fig. 1. pH-values in the lakes studied.

The only macrobenthic crustacean that has so far been found in acid lakes is *Asellus aquaticus*. However, in waters with pH-values around 4 (Lake Trollkarlen) even this animal seems to disappear (Grahn *et al.* 1974, Wiederholm and Eriksson 1977).

In normal lakes Odonata usually occur only in small numbers, but in the lakes studied they were remarkably abundant in the bottom samples taken. The abundance is probably due mainly to a reduced predation by fish. This agrees with the findings of Grahn *et al.* 1974.

One of the most pH-tolerant species seems to be *Sialis lutaria* (Megaloptera), also found by Parson (1968) in extremely acid water (pH 2.8). This species also occurs in large numbers even in the most acid lakes in the present material.

Species of the order Heteroptera are known to be favoured by the absence of fish predation (Macan 1965, Henrikson and Oscarsson 1978) and can be found in large numbers in acid waters. These animals are free-swimming and very active and cannot be quantitatively sampled by the method used. Consequently they occur more frequently in the lakes studied than would appear from the tables.

Among Trichoptera the most tolerant species seem to be *Cyrnus flavidus* and *Holocentropus dubius*, but it is obvious that even *Agrypnia varia* can survive at low pH-values. The abundance of Trichoptera is not remarkably high in the present material. Species of this order are known to be susceptible to fish predation and have sometimes been reported to be abundant in acid waters (Grahn *et al.* 1974).

In the deepest parts of many of the lakes investigated, the fauna is dominated by *Chaoborus flavicans* (Diptera, Chaoboridae). This is due to the ability of this animal to tolerate low concentrations of oxygen (Peus 1934).

Along with that species, *Chaoborus obscuripes* occurs in Lakes Iglafallssjön, Blanksjön, Vibollsjön and Trehörningen. In May-June this species could be observed in dense swarms all along the shores of the lakes. Owing to the behaviour of these species the number of Chaoboridae has been underestimated in the samples in the same way as has that of the species of Heteroptera. The fact that *C. obscuripes* is absent in lakes with normal fish populations must be due to a high predation pressure. *C. flavicans*, on the other hand, lives mainly at depths where predation by fish is of less importance (Stenson 1978). The lack of Chaoboridae in Lake Trollkarlen may be explained by the low pH in that lake, although other factors may be more probable.

Two genera Tanypodinae (Diptera, Chironomidae), *Ablabesmyia* and *Procladius* are frequently met with in the lakes. Both genera are eurytopic and are known from different types of lakes (Brundin 1949, Fittkau 1962).

Larvae of the subfamily Orthocladinae found in acid lakes (*e.g. Heterotrissochladius marcidus* and *Zalutschia zalutschicola*) are those generally occurring in humic waters. Saether (1976) suggests that *Zalutschia potamophilus* (described as larvae) may possibly be identical with *Zalutschia mucronata* (described as adult). *Z. mucronata* was earlier found in polyhumic lakes (Brundin 1949) and in acid lakes (Mossberg, unpubl.). The occurrence of *Z. potamophilus* in the present lakes tends to confirm the hypothesis that the species are identical. If they are, *Z. mucronata/potamophilus* seems to be a species typical for acid lakes. Another genus that is common in humic waters and occurs even in acid lakes is *Psectrocladius*.

As can be seen from the tables, species of *Chironomus* (Chironominae) are very common in acid lakes and the occurrence of the genus increases with decreasing pH. This is especially noticeable in the littoral zone of the most acid lake, where 86 per cent of the fauna consisted of *Chironomus* (Fig. 2). At greater depths of lakes of the type at issue, but with normal pH-values, *Phaenopsectra sp.* should dominate the bottom fauna (Brundin 1949). This is in fact valid for the least acid lakes in the present material, but at a pH around 4.5 this species is replaced by *Chironomus sp* (Fig. 3). The big difference in species dominance which exists between Lakes Svartsjön and Långsjön, in spite of equal pH-values, may be explained by the more extreme pH conditions in the former lake during spring (Fig. 1). The genus *Chironomus* is apparently generally able to adjust to very extreme environments. It is abundant in polluted lakes with low concentrations of oxygen and high pH-values as well as in very acid waters (pH 2.3—3.2) (Harp and Campbell 1967).

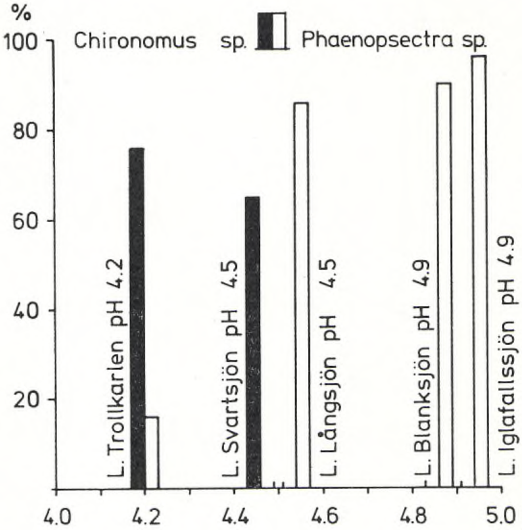

Fig. 3. Relative importance (in percent of total fauna) of *Chironomus sp.* and *Phaenopsectra sp.* at 6—10 m depth in five of the lakes.

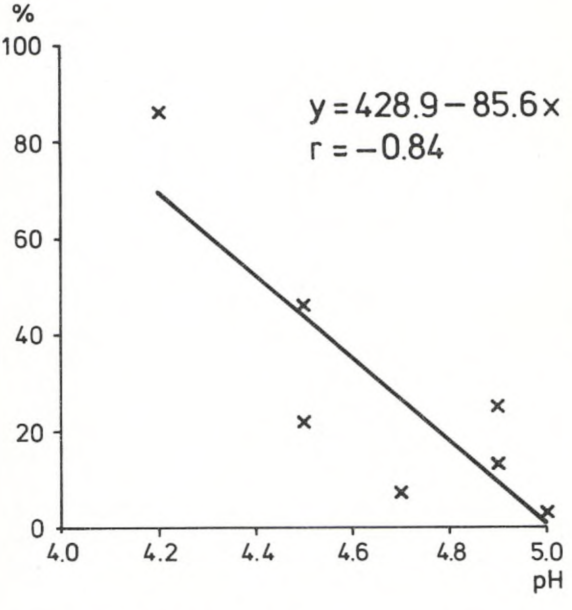

Fig. 2. Relative number of *Chironomus sp.* in the littoral zone (1 and 2 m) in relation to pH. (In per cent of total fauna.)

Other chironomids typical for normal oligotrophic and oligohumic lakes are Tanytarsini (Brundin 1949). However, in the acid lakes here investigated this groups is of minor importance.

Earlier studies have shown that the number of species as well as the number of individuals decreases with increasing acidity (Leivestad *et al.* 1976). Results presented in Fig. 4 indicate a correlation between pH and number of taxa. On the other hand, there does not seem to be any correlation between number of individuals and pH.

The composition of the benthos in the seven lakes is of the same type as in humic waters. Typical species are, for example, *Leptophlebia vespertina*, *Leucorrhinia dubia*, *Zalutschia zalutschicola* and *Phaenopsectra longiventris* (Brundin 1949, Berg and Petersen 1956, Corbet *et al.* 1960). These findings are also in good agreement

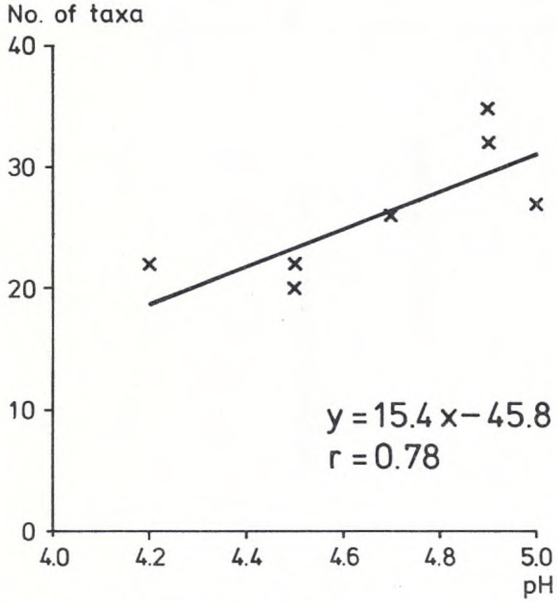

Fig. 4. Number of taxa in relation to pH.

with WIEDERHOLM and ERIKSSON (1977). The most remarkable difference from the humic lake type is the pronounced development of species of the genus *Chironomus* with increasing acidity.

V. SUMMARY

The structure of the benthic community was studied in seven small (1.6—11.5 ha) acid (pH-mean: 4.2—5.0) forest lakes. All of these lakes can be considered to be practically empty of fish at the time of sampling.

There was a clear tendency for the number of taxa to decrease with increasing acidity. Only one species of each of the orders Hirudinea, Ephemeroptera and Mollusca was found.

The bentic community of the lakes was dominated by the order Diptera (*e.g.* Chaoboridae and Chironomidae). The species composition of the benthos in the lakes studied was very much the same as is found in humic waters, but in the most acid lakes the greater part of the chironomid fauna consisted of *Chironomus sp.*

Probably as a result of the very slight or non-existent fish predation, certain groups of animals (*e.g.* Odonata, Heteroptera and Chaoboridae) occurred in unusual abundance.

VI. ACKNOWLEDGMENTS

Analyses of nitrogen and phosphorus were performed by the National Swedish Environment Protection Board. The study was financed by the Fishery Board of Sweden and the Central Operating Management (joint organization of major Swedish power producers).

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Catch/Temperature Relationship in Fish Species in a Brackish Heated Effluent

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CONTENTS

I. INTRODUCTION

In several investigations heated effluents from power plants have been shown to effect the behaviour of fish. The primary reactions of the fish are attraction or repulsion and a changed level of activity. In the theory the fish moves towards its "temperature preferendum", where, according to FRY (1971), the amount of energy available for activity reaches its maximum. The principal aim of the study presented here was to arrange the Baltic coastal fishes in a scale, ranging from cold- to warm-water species, which could be used to predict reactions of the fish fauna to heated effluents. The grouping of species has been achieved by studying the relationship catch/temperature for a trap and for gill nets at a cooling water outlet before and after the starting up of the power plant. The catch in a stationary tool integrates attraction/repulsion and activity as it depends both on the number of fish around the tool and on their activity.

II. THE INVESTIGATION AREA

The investigation was carried out at the first commercial nuclear power plant in Sweden, Oskarshamnsverket at Simpevarp. This plant is situated on the Baltic coast 20 km north-east of Oskarshamn (Fig. 1). The first unit was brought into operation at the beginning of 1972. It has an output of 460 MW, requiring 22 m^3 of cooling water per second, heated 8—12°C. A second unit producing 580 MW, was started in the autumn of 1974. The water, totalling 50 m^3/sec, is discharged at the southern shore of the almost landlocked bay Hamnefjärden (Fig. 1). The only connection between this bay and the sea is the channel Hamnehålet, which opens out in the middle of an open stretch of coast with a length of two nautical miles. The temperature reduction of the cooling water between the point of discharge and Hamnehålet is insignificant, owing to the rather high velocity of the water. Inside the point of discharge, however, the currents are very weak, and the water is gradually cooled to only a few degrees above the ambient temperature in the innermost parts of the bay.

The inner part of Hamnehålet has a width of 30 metres and a maximum depth of three metres. The greatest depth of the bay, seven metres, is found just inside this sill; the rest of the bay is mostly between two and five metres deep. The

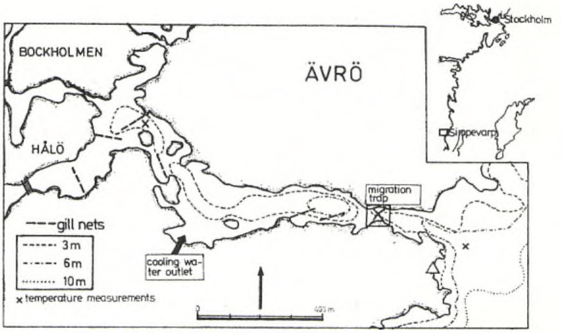

Fig. 1. Site of the study area, around the nuclear plant of Simpevarp.

depth of the water off the coast is for several nautical miles seawards only 10—20 metres. In Hamnefjärden soft bottom prevails but the shores consist mainly of rocks and stones. The benthic vegetation is sparse; in some indentations there are narrow belts of *Phragmites* and in the deeper places *Myriophyllum* and species of *Potamogeton* are predominant. The shores outside Hamnehålet are rocky and exposed, with a vegetation dominated by *Dichtyosiphon foeniculaceus, Fucus vesiculosus, Cladophora* and *Enteromorpha.*

The salinity of the surface water off Simpevarp and in Hamnefjärden is slightly higher than 7 ‰ on average.[1] During middle and late summer the temperature is normally about 15°C. It is as a rule fairly homogeneous down to 20 metres depth. Under natural conditions the horizontal temperature gradients, too, are small in the open sea. In Hamnefjärden, however, the surface water during summer is considerably warmer than both the water near the bottom and the surface water at sea. This shows that the interchange between the bay and the sea is limited. Outside the bay the temperature variations over time may be large. When, during summer, offshore winds cause upwellings, variations of several degrees per hour have been observed.

The original fish fauna in the area has been described by NEUMAN (1974 a). Hamnefjärden is dominated by perch (*Perca fluviatilis* L.) and roach (*Rutilus rutilus* (L.)) and other freshwater species. These species spawn in the bay, which probably also serves as spawning ground for the adjacent open coast. Outside Hamnefjärden freshwater fish are common close to the shore, but further out marine species such as herring (*Clupea harengus* L.) and cod (*Gadus morhua* (L.)) predominate.

III. METHODS

This paper deals with catches in a migration trap in Hamnehålet and in gill nets in Hamnefjärden. These tools were in operation both before and after the starting up of the power plant.

The migration trap

The fish migration through Hamnehålet was studied with the use of two pound nets placed on the sill, which has a maximum depth of three metres, between Hamnefjärden and the sea. One net caught the ingoing fish, the other the outgoing ones. The whole depth was barred even at high water. The design and dimensions of the trap are shown in Fig. 2. In the fyke net there are three almost square entrances, the last of which has a side of 10 cm. The meshes have a height of 28 mm in the arms and 24 mm in the enclosure. Thereafter they gradually decrease to 12 mm at the end of the fyke net, a dimension which should not give any selectivity of size for specimens of fusiform fish longer than 10 cm.

The central part of the trap was fixed to a steel-pipe construction, and the leaders were held up by wires across the passage. Extensive arrangements for holding the nets to the bottom were necessitated by the fact that when the cooling water pumps operated, the nets became covered with algal filaments, mud, etc. As a result the water pressure on the nets was many times increased. This made it necessary to lift and clean the leaders once a week during summer and autumn.

The trap was emptied once daily Monday to Friday. The examining of the nets usually started at 8.30 a.m. and lasted, as a rule, for one hour at the most. The fish was registered as to species and direction of migration and also as to length group (total length, the caudal fin stretched), a class width of 5 cm being applied. After the fish

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[1] Hydrographic data from BERGSTRAND (1969).

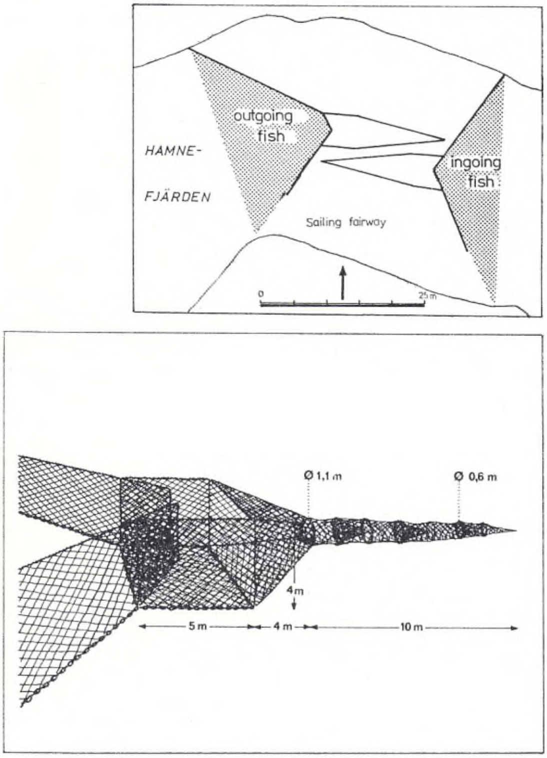

Fig. 2. Situation and design of the traps at the mouth of Hamnefjärden.

had been noted it was carried past the trap in its migratory direction in a tub filled with water or in a fish chest, and was then released some 10 metres from the trap. The observed mortality was low. In connection with the emptying of the trap the water temperature was measured at the surface and bottom close to the nets and also at one locality in the inner part of Hamnefjärden and one outside Hamnehålet (Fig. 1).

The trap was in operation during the following periods: June 26—December 19, 1970, February 22—26, 1971, March 8—July 5, 1971, July 20—29, 1971, September 21, 1971—June 1, 1972, June 16—September 5, 1972 and September 12, 1972—June 29, 1973.

During summer it was necessary to keep open a sailing fairway (7 m wide) along the southern shore of Hamnehålet (Fig. 2). This channel was open June 26—October 16, 1970, and June 24—September 20, 1971. During the summer of 1972 and in June 1973 it was open during the weekends only.

The fishing in Hamnefjärden

The fishing in Hamnefjärden started in 1966 and is still going on. It is carried out with fixed combinations of bottom gill nets with different mesh sizes. Eighteen nets made of spun nylon are used. They have a length of 30 metres and, in the water, a height of 1.5 metres (6-foot nets). The following mesh sizes were used:

mesh size	10[1]	12	16	18	20	24	28[2]	rows/ell
number of nets	2	2	2	4	4	2	2	

[1] 60 mm [2] 21 mm

The nets are always placed at the same stations and in the same order (Fig. 1, more in detail in THORESSON 1977). They are set between 3 and 5 p.m. and lifted between 7 and 9 a.m. on the following day. Number and total weight are noted for each species and net. In the period 1966—69 only 10 species, among them the most common ones, were registered. Before 1972 the surface temperature at one point in Hamnefjärden was measured at the lifting of the nets. Since then the bottom temperature at each net has been registered both at setting and lifting.

During the period 1966—69 one setting was carried out in each of the months May, June, August, September and October. In 1970 and 1971 together 38 settings were made during the period May to December. During 1972—76, the last period treated here, the fishing was carried out once a week.

IV. RESULTS

The results are presented in four main sections. The first of these reports for the total catches and their distribution between species. In the second section the catches in the migration trap are related to season and temperature and in the third to the operation of the power plant. The fourth section treats the net fishing in Hamnefjärden.

The composition of the catches

The total catches are shown in Table 1. For the migration trap they amounted to 377,176 fishes belonging to 32 species. The corresponding figures

Table 1. *The catches and their percentage distribution between species.*

		Migration trap 1970—73				Gill nets 1972—76	
		In	Out	Total	Composition	Number	Composition (%)
Freshwater species:							
Perch	*Perca fluviatilis* L.	71,663	73,244	144,907	39.4	12,407	41.8
Stickleback	*Gasterosteus aculeatus* L.	31,153	17,849	49,002	13.0	—	—
Ruffe	*Gymnocephalus cernua* (L.)	1,673	4,691	6,364	1.7	1,652	5.6
Smelt	*Osmerus eperlanus* (L.)	635	662	1,297	0.3	4	0.0
Burbot	*Lota lota* (L.)	159	171	330	0.1	37	0.1
Whitefish	*Coregonus lavaretus* (L.)	34	94	128	0.0	13	0.0
Pike	*Esox lucius* L.	69	56	125	0.0	190	0.6
Trout	*Salmo trutta* L.	23	85	108 [1]	0.0	92	0.3
Salmon	*Salmo salar* L.	7	78	85 [1]	0.0	5	0.0
Cyprinids:							
Roach	*Rutilus rutilus* (L.)	91,795	35,908	127,703	33.9	8,936	30.1
Silver bream	*Blicca bjoerkna* (L.)	16,431	4,669	21,100	5.6	3,232	10.9
Bleak	*Alburnus alburnus* (L.)	11,555	2,340	13,895	3.7	2	0.0
Ide	*Leuciscus idus* (L.)	1,576	303	1,879	0.5	388	1.3
Zanthe	*Vimba vimba* (L.)	918	583	1,501	0.4	221	0.7
Rudd	*Scardinius erythrophthalmus* (L.)	687	264	951	0.3	646	2.2
Bream	*Abramis brama* (L.)	489	67	556	0.1	165	0.6
Tench	*Tinca tinca* (L.)	1	2	3	0.0	5	0.0
Crucian carp	*Carassius carassius* (L.)	2	0	2	0.0	—	—
Dace	*Leuciscus leuciscus* (L.)	—	—	—	—	3	0.0
Marine species:							
Flounder	*Platichthys flesus* (L.)	782	2,565	3,347	0.9	1,200	4.0
Sea scorpion	*Myoxocephalus scorpius* (L.)	554	634	1,188	0.3	323	1.1
Herring	*Clupea harengus* L.	231	778	1,009	0.3	121	0.4
Eel pout	*Zoarces viviparus* (L.)	303	581	884	0.2	—	—
Eel	*Anguilla anguilla* (L.)	202	144	346	0.1	19	0.1
Sprat	*Clupea sprattus* (L.)	92	80	172	0.0	—	—
Cod	*Gadus morhua* (L.)	32	109	141	0.0	10	0.0
Black goby	*Gobius niger* L.	16	20	36	0.0	3	0.0
Turbot	*Scophthalmus maximus* (L.)	3	19	22	0.0	15	0.1
Lumpsucker	*Cyclopterus lumpus* L.	12	8	20	0.0	1	0.0
Father lasher	*Cottus bubalis* Euphrasén	2	7	9	0.0	8	0.0
Fourhorn sculpin	*Oncocottus quadricornis* (L.)	1	1	2	0.0	—	—
Sand eel	*Ammodytes lancea* (L.)	1	2	3	0.0	—	—
Twaite shad	*Alosa fallax* (LACÉPÈDE)	0	1	1	0.0	—	—
	Sum:	231,101	146,015	377,116	—	29,698	—

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[1] Most of these fish originate from introductions of reared fish in the bay.

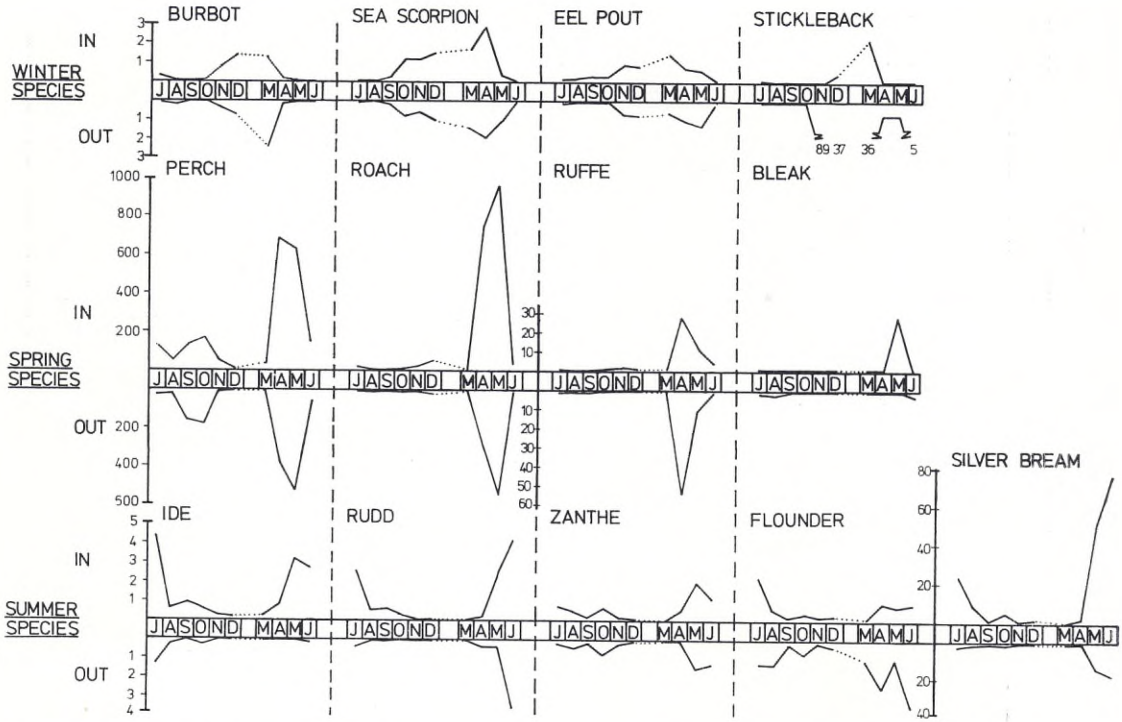

Fig. 3. The seasonal distribution of catches. Mean daily catches July 1970—June 1971.

for the "natural" year July 1970—June 1971 are 179,795 and 27. The catches in the gill nets during the period after the starting up of the power plant, 1972—76, consisted of 29,698 fishes of 26 species. For the years 1966—71, when only 10 species were registered, the total is 6,277. As can be seen in Table 1, there is a massive predominance of freshwater species, amounting to about 98 % (including stickleback) in the trap and 94 % in the nets. Perch and roach have a prominent position, together accounting for more than 70 % in both tools. Other species frequently caught in the trap are silver bream, stickleback, ruffe and bleak. With regard to stickleback it should be pointed out, that owing to its small size only a tiny proportion of the sticklebacks passing through Hamnehålet are caught. For the same reason there is also a considerable loss of bleak. An analysis of the length distribution of the catches indicates that most fishes shorter than 10 cm are not caught. Stickleback and bleak are not caught at all by the gill nets, which have no meshes finer than 21 mm. Among the marine species, flounder and sea scorpion gave the biggest catches in both tools.

As regards species composition there is considerable similarity between the catches in the trap on the sill between the open sea and the sheltered bay and those in the nets within this bay. Such differences as exist are largely attributable to the lower size selectivity of the trap. The fish community outlined above contrasts sharply with that existing some hundred metres seawards, where herring and cod predominate (NEUMAN 1974 a).

The catches in the migration trap in relation to season and temperature

The mean daily catches of the most frequently caught species in the period July 1970—June 1971 are given in Fig. 3, separately for each month and for in- and outgoing fish. The last few days of February have been transferred to March. On the basis of Fig. 3, the common species may be arranged in three groups with catch maxima

Table 2. *Winter catches in fyke nets.*

January 14—February 18	Burbot	Eel pout	Sea scorpion	Perch	Ruffe
Number	59	49	41	4	1

These values are not used in any other context.

during winter (including late autumn and early spring), spring and summer respectively. As has been mentioned under "Methods" a sailing fairway was kept open during the summer (Fig. 2). This means that the summer catches must give an underestimation of the migration. This should not, however, affect the grouping.

Burbot, *sea scorpion*, *eel pout* and *stickleback* belong to the winter group. The winter catch of burbot seems to be connected with spawning in Hamnefjärden. At the end of 1970, ingoing fish can be seen to predominate, but in March after the spawning at the beginning of the year, there is a predominance of outgoing fish. In January and February 1971, when the pound nets were out of operation owing to difficult ice conditions, four small, fine-meshed, fyke nets were set in their place. The catches of these traps are sample tests of the migrations of bottom fish (Table 2) indicating a rather high activity of burbot, sea scorpion and eel pout in the middle of the winter. The sea scorpion spawn in the autumn and the fry of the eel pout is born around the turn of the year (ANDERSSON 1964). The stickleback seems to emigrate from Hamnefjärden during late autumn and winter. As mentioned above, however, the value of the results is limited by the small size of this species; for that reason it is not further treated in this paper.

Perch, *roach*, *ruffe* and *bleak* give the largest catches during spring. Perch, however, also has a peak during the autumn. Perch, roach and ruffe spawn mainly in May, bleak mainly in June. Thus the catches are concentrated within the spawning time and the weeks immediately proceeding this.

The cyprinids *silver bream*, *ide*, *rudd* and *zanthe*, as well as *flounder*, are mainly caught during summer and late spring. The spawning activity is reflected in the catches of silver bream and rudd, which spawn in June—July and June respectively. This is not the case with the other species. According to ANDERSSON (1964) ide and zanthe spawn in rivulets in March—April and March—July respectively, while flounder spawn in deeper areas during spring and early summer. The flounder is reported to remain in shallow water in the summer but to leave the coast in the winter.

The relationship between catch and temperature has been studied by calculating the mean catch per day for ingoing fish within temperature intervals of 2°C. The bottom temperature at the trap was measured on the occasion of emptying. Monday data were excluded, since they represent three days of migration. The calculations have been done separately for the periods January—June and July—December for each of the years 1970—73 in order to distinguish between the warming-up and cooling-down periods and the two parts of the light cycle. The results are presented in Table 3 and, for some species, also in Fig. 4.

A classification of species done according to the catch/temperature relation is of course similar to that based on the seasonal distribution. Catches of *burbot*, *sea scorpion* and *eel pout* take place primarily at temperatures below 6°C. At high temperatures — more than 18°C — these species are not caught at all. Ruffe is caught predominantly at low temperatures at the beginning of the year, but catches also occur in warm water. *Perch* and *roach* give large catches within a wide spectrum from low to high temperatures. Large migrations at low temperatures at the beginning of the year occur in connection with the spawning. The cyprinids, with the exception of roach, and *flounder* are mainly caught at high or medium — high temperatures (more than 6°C).

In 1972 and 1973 the power plant discharged heated water during most of the year (see Fig. 5). During the summer of 1972 it was not in operation, but that summer was considerably warmer than those of 1970 and 1971. The "cold water species" — burbot, sea scorpion and eel pout — show about the same distribution of catches along the temperature scale before and after the starting up of the power plant. This indicates an avoidance of high temperatures. For most of the

Table 3. *Catches within intervals of temperature.*

Temperature (°C)		0	2	4	6	8	10	12	14	16	18	20	22	24	26
Number of catch days															
1st half-year	1971	33	14	8	4	8	5	20	—	—	—	—	—	—	
	1972	26	8	13	12	41	18	8	(1)	(2)	—	—	—	—	
	1973	(2)	5	4	10	13	34	47	11	(1)	—	—	—	—	
2nd half-year		(1)	23	17	11	19	28	8	8	7	—	(3)	—	(2)	
	1972	(0)	(1)	9	(1)	4	(2)	14	13	23	32	21	6	4	
Mean daily catches of ingoing fish (intervals with < 4 days excluded).															
Burbot	1971	1.5	0.1	0.0	0.0	0.0	0.0	0.0	—	—	—	—	—	—	
1	1972	0.2	0.3	0.2	0.5	0.4	0.1	0.0	—	—	—	—	—	—	
	1973	—	0.0	0.0	0.0	0.0	0.0	0.1	0.0	—	—	—	—	—	
2	1970	—	1.2	0.2	0.5	0.1	0.0	0.0	0.0	0.0	—	—	—	—	
	1972	—	—	0.3	—	0.3	—	0.1	0.0	0.0	0.0	0.0	0.0	0.0	
Sea scorpion	1971	2.2	4.5	1.2	0.5	0.4	0.2	0.2	—	—	—	—	—	—	
1	1972	1.6	3.1	1.5	1.2	1.0	0.7	0.1	—	—	—	—	—	—	
	1973	—	0.2	0.3	0.1	0.3	0.1	0.0	0.1	—	—	—	—	—	
2	1970	—	0.0	2.4	0.9	1.5	0.4	0.0	0.1	0.0	—	—	—	—	
	1972	—	—	1.6	—	0.5	—	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
Eel pout	1971	1.8	1.0	1.0	1.0	0.9	0.0	0.1	—	—	—	—	—	—	
1	1972	0.7	0.8	1.5	1.0	0.3	0.4	0.1	—	—	—	—	—	—	
	1973	—	1.2	1.0	0.0	0.0	0.2	0.3	0.0	—	—	—	—	—	
2	1970	—	1.4	0.9	0.4	0.2	0.2	0.0	0.2	0.2	—	—	—	—	
	1972	—	—	0.9	—	0.3	—	0.1	0.1	0.0	0.0	0.0	0.0	0.0	
Ruffe	1971	2.1	33	29	16	15	14	6.5	—	—	—	—	—	—	
1	1972	1.8	0.5	1.2	1.3	1.2	0.4	0.1	—	—	—	—	—	—	
	1973	—	0.0	0.0	0.2	0.6	0.4	0.4	0.6	—	—	—	—	—	
2	1970	—	2.0	2.1	3.0	1.7	0.7	0.4	0.4	0.0	—	—	—	—	
	1972	—	—	0.2	—	0.8	—	0.1	0.0	0.9	0.6	0.5	0.0	0.0	
Perch	1971	34	800	1,000	590	920	670	190	—	—	—	—	—	—	
1	1972	20	35	64	17	67	79	15	—	—	—	—	—	—	
	1973	—	12	4.5	25	50	29	28	36	—	—	—	—	—	
2	1970	—	20	130	380	170	170	140	120	60	—	—	—	—	
	1972	—	—	4.2	—	12	—	25	9.3	34	37	12	3.3	7.3	
Roach	1971	4.2	1,200	1,700	2,200	370	200	28	—	—	—	—	—	—	
1	1972	59	28	460	160	110	74	340	—	—	—	—	—	—	
	1973	—	45	270	570	330	54	32	140	—	—	—	—	—	
2	1970	—	65	27	27	19	18	31	19	11	—	—	—	—	
	1972	—	—	9.4	—	49	—	26	36	29	36	31	73	35	

Table 3. Continued.		0	2	4	6	8	10	12	14	16	18	20	22	24	26
Bleak	1971	0.0	0.1	0.5	73	52	2.6	4.1	—	—	—	—	—	—	
1	1972	1.8	0.0	6.1	38	9.7	4.9	0.5	—	—	—	—	—	—	
	1973	—	0.8	9.0	4.7	8.6	20	18	14	—	—	—	—	—	
2	1970	—	0.4	3.0	3.8	3.3	2.5	0.4	0.5	0.6	—	—	—	—	
	1972	—	—	0.7	—	6.5	—	6.2	35	6.1	11	58	177	4.0	
Flounder	1971	0.1	1.2	1.1	0.5	1.0	1.0	1.2	—	—	—	—	—	—	
1	1972	1.0	2.5	1.1	0.8	2.8	1.4	1.1	—	—	—	—	—	—	
	1973	0.0	1.0	0.3	0.6	1.4	1.0	0.3	0.8	—	—	—	—	—	
2	1970	—	0.2	1.3	2.0	1.8	0.9	0.4	0.8	0.0	—	—	—	—	
	1972	—	—	1.1	—	3.0	—	0.9	0.5	1.4	0.5	3.2	0.0	0.3	
Rudd	1971	0.0	0.4	1.8	—	3.5	6.2	5.9	—	—	—	—	—	—	
1	1972	0.1	0.4	0.0	0.3	0.2	0.4	0.5	—	—	—	—	—	—	
	1973	—	0.0	0.0	0.1	1.2	0.6	0.8	3.8	—	—	—	—	—	
2	1970	—	0.0	1.6	1.2	1.0	1.5	2.8	0.8	0.4	—	—	—	—	
	1972	—	—	0.0	—	0.0	—	0.0	1.9	1.4	0.4	0.2	1.7	0.8	
Ide	1971	0.4	1.0	1.7	5.7	5.5	1.6	3.7	—	—	—	—	—	—	
1	1972	0.4	0.4	0.6	1.2	2.3	0.9	2.5	—	—	—	—	—	—	
	1973	—	0.2	0.3	3.4	4.6	2.9	1.1	2.6	—	—	—	—	—	
2	1970	—	0.4	4.8	2.4	2.1	2.2	2.3	1.0	0.1	—	—	—	—	
	1972	—	—	0.7	—	1.8	—	1.2	4.8	1.3	3.3	5.4	6.0	12	
Zanthe	1971	0.1	0.4	1.5	3.2	3.6	0.3	1.6	—	—	—	—	—	—	
1	1972	0.9	0.0	0.1	1.1	3.3	0.9	0.4	—	—	—	—	—	—	
	1973	—	0.0	0.3	1.8	6.9	1.6	0.4	0.7	—	—	—	—	—	
2	1970	—	0.3	0.6	0.8	0.7	0.8	1.4	1.0	0.6	—	—	—	—	
	1972	—	—	0.1	—	0.0	—	0.8	1.7	2.8	3.3	1.4	0.8	2.0	
Silver bream	1971	0.1	2.4	25	42	81	96	100	—	—	—	—	—	—	
1	1972	6.5	0.1	1.9	8.9	24	21	28	—	—	—	—	—	—	
	1973	—	0.0	1.8	9.5	31	23	6.7	13.1	—	—	—	—	—	
2	1970	—	1.9	10	17	15	16	13	7.3	4.4	—	—	—	—	
	1972	—	—	1.2	—	7.3	—	13	44	84	54	18	110	48	

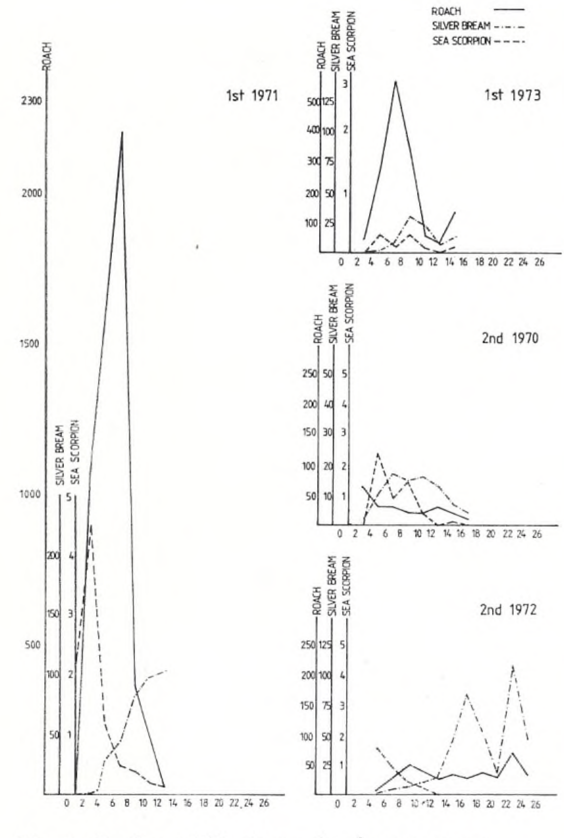

Fig. 4. Catches within intervals of temperature.

other species, too, the changes are rather small during the first half-year. During the second, however, there is in most cases a clear shift of the catches towards higher temperatures. This indicates that the relation between behaviour and temperature is more rigid at the beginning of the year, and presumably is especially so in connection with the spawning.

The effect of streaming and heated water on the migrations

In analysing the effects of the operating of the power station on the migrations, the aim has been to separate the influence of current and heating. It was possible to test this because the cooling water pumps were run for a long period before the production of electricity was started and also during the frequent short interruptions of the production. Thus it has been possible to compare the catches during the following three situations: (1) long periods without pumping, mostly before the start, (2) pumping of unheated water and (3) pumping of heated water. Situation (1) encompasses the periods July 1970—April 1971 and June—July 1972. In May 1971 pumping of unheated water started and it took place intermittently during the summer and almost continuously from October. At the end of the year the water was sometimes slightly heated. High effects, classified as situation (3), are noted for January 1972. The production of electrical energy, roughly equalling half of the heat energy transmitted to the cooling water, is shown in Fig. 5. During the period when the migration trap was in operation, October 1972 is the only month without any interruption of the heating. As can be seen, there was a long interruption during the period May—August 1972. June and July have been classified as (1), while May lies too close to the production of electricity and August is disturbed by pumping.

In Fig. 6 the mean daily catch is shown for the three situations mentioned above. The values for each month are shown in order to make the comparisons less influenced by factors irrelevant in this context. The figures for outgoing fish are difficult to interpret, since a big catch may indi-

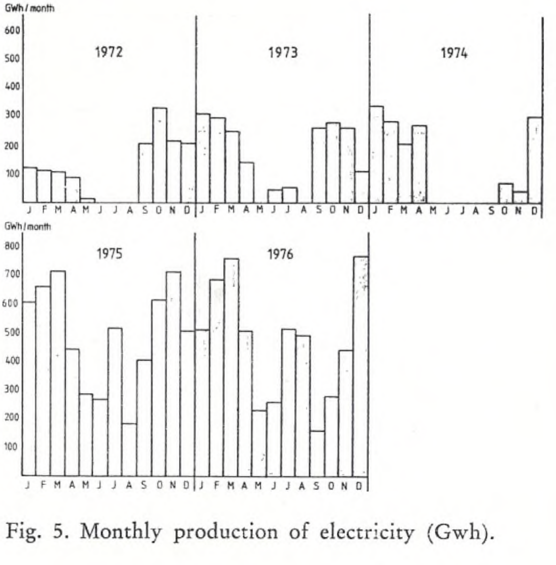

Fig. 5. Monthly production of electricity (Gwh).

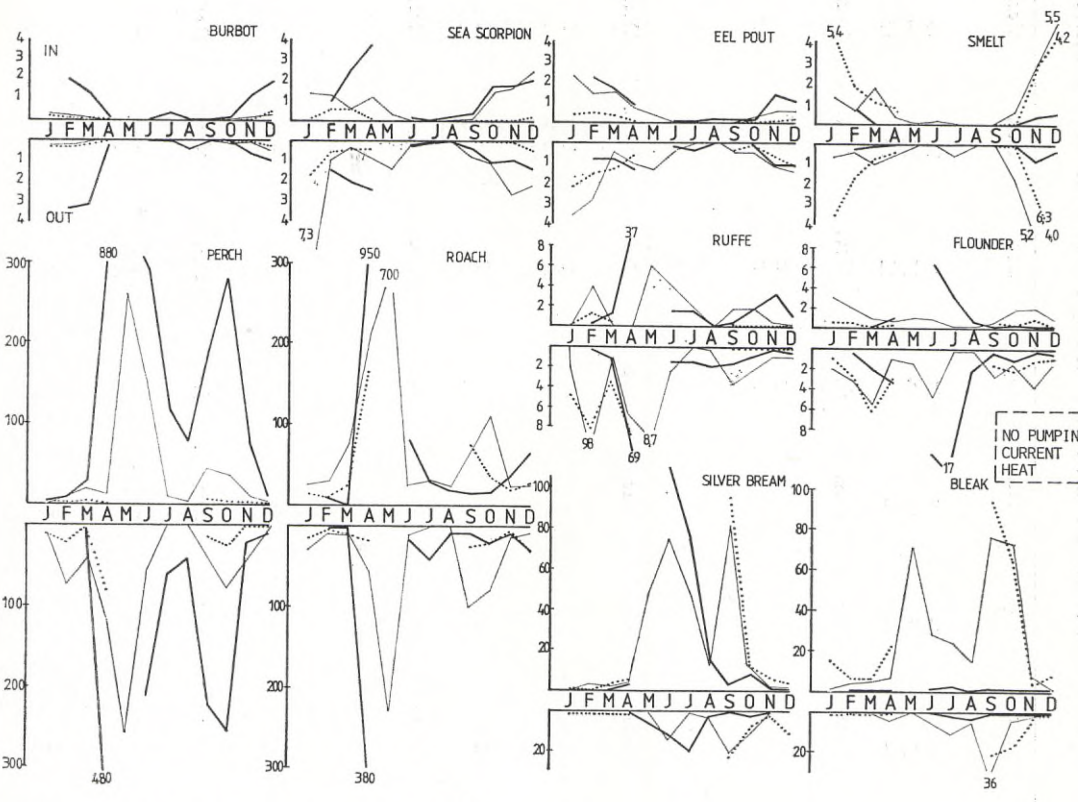

Fig. 6. The effects of current and heat. Mean daily catches.

cate either an increased level of activity in Hamnefjärden or a repulsion from the cooling water. The catches of ingoing fish are more useful, since here attraction-repulsion and activity work in the same direction.

The effects of current and heating have been statistically tested by comparing the monthly mean values for current and no pumping, on one hand, and those for heating and current on the other, by means of a t-test. WELCH's (1937) method was adopted where the variances were significantly different and STUDENT's (1908) in other cases. The results are entered in Table 4. It should be noted that the comparisons between different situations suffer from the impossibility of estimating the natural variations between years.

The current drastically reduces the catches of *burbot*. The effects on *sea scorpion* and *eel pout* are not so strong, but decreases predominate among the significant differences except in the case of the emigration in the autumn. The heating of the water causes a further decrease of the catches. This is most evident for ingoing eel pout; the catches of burbot are already very small on account of the current.

The reactions of *ruffe* to the current differ according to the season. The high figure for outgoing fish in streaming water in February is mainly accounted for by a single day, a matter which is further treated below. With one exception all significant differences between current and heating are negative. Both current and heating decrease the migration of *perch* in both directions. The only significant increase concerns "Out" in streaming water in March. This rather high value and the corresponding one for February have been found to be caused by a few days with big catches, which are discussed further below. The catches of both in- and outgoing *roach* seem to have increased in streaming water

Table 4. *The effects of current and heating.* The table shows the significant (5 %) differences between daily catches during: (1) long periods without pumping as compared with pumping of unheated water (C in the table) and 2) pumping of unheated as compared with heated water (H in the table). + after C denotes a significant increase in current and after H in heat. — denotes decreases and 0 non-significant relations. The absence of signs means lack of observations — less than 5 per situation per month.

	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Number of observations (at least 5 per month).												
No pumping	—	5	17	19	—	16	44	19	22	22	21	15
Current	6	9	6	16	18	25	5	17	5	17	29	29
Heat	30	28	27	16	—	—	—	—	13	22	14	13
Burbot	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.	Nov.	Nov.	Dec.
In												
C		0	—	0		0	0	0	0	0	—	—
H	0	0	0	0					0	0	—	0
Out												
C		—	—	—		0	0	0	0	0	—	0
H	0	0	+	—					0	0	0	—
Sea scorpion	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
In												
C		0	—	—		—	0	—	—	0	0	0
H	0	0	0	—					0	—	—	—
Out												
C		0	—	—		0	0	0	0	0	+	0
H	0	0	0	0					0	—	—	—
Eel pout	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
In												
C		0	0	0		0	0	—	—	0	—	—
H	—	—	—	—					0	—	—	—
Out												
C		0	0	0		0	0	0	+	+	0	0
H	0	0	0	0					0	—	0	—
Ruffe	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
In												
C		+	—	—		+	0	—	0	0	—	—
H	0	—	0	0					0	—	—	—
Out												
C		0	0	—		0	—	—	+	+	+	+
H	0	0	+	0					—	—	—	0

Table 4. Continued.

Perch	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
In												
C		0	0	–		–	–	–	–	–	–	–
H	0	–	–	–					0	–	0	–
Out												
C		0	+	–		–	–	–	–	–	0	0
H	0	–	–	0					0	–	–	–
Roach	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
In												
C		0	+	–		–	0	0	+	+	0	0
H	0	–	–	0					0	–	0	0
Out												
C		+	0	–		–	–	0	0	+	0	0
H	0	0	0	0					–	–	–	0
Flounder	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
In												
C		0	0	0		–	0	0	+	+	+	+
H	–	0	0	0					0	–	0	0
Out												
C		+	+	–		0	–	–	+	0	+	+
H	0	0	0	+					0	0	–	0
Silver bream	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
In												
C		0	+	–		–	0	0	+	0	0	0
H	+	0	0	+					0	0	+	+
Out												
C		+	+	+		0	0	0	+	+	+	0
H	0	0	0	–					0	0	0	0
Bleak	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
In												
C		0	0	+		+	+	0	+	+	+	0
H	+	0	0	+					0	0	–	+
Out												
C		0	0	0		+	0	0	0	+	0	0
H	0	0	0	0					0	0	0	0
Smelt	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
In												
C		0	+	0		0	0	0	0	+	+	+
H	+	0	0	0					0	–	0	0
Out												
C		0	+	+		0	0	0	0	0	+	+
H	+	+	0	0					0	0	0	0

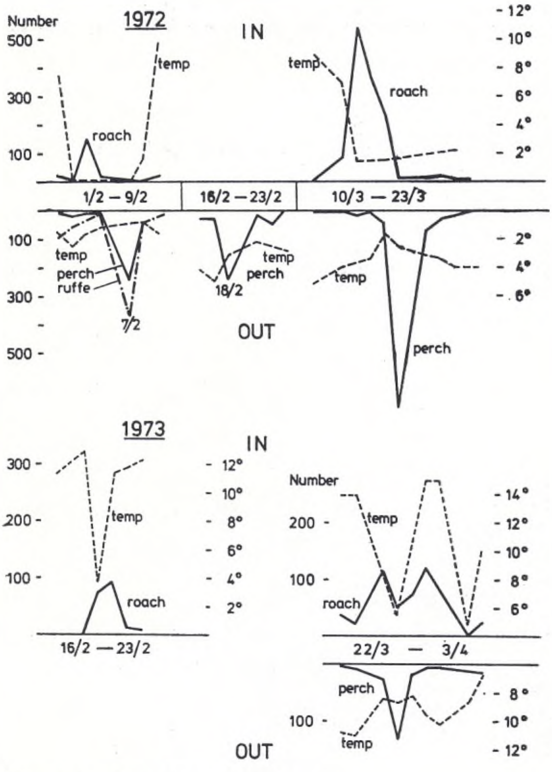

Fig. 7. Catch peaks during the winter.

during the winter and in September—October. The opposite is true for the period around the spawning, April and June — for May there is no reference material. During the rest of the year the differences are rather small. The heating has a comparatively small but predominantly negative effect.

The above-noted big catches of outgoing perch and ingoing roach in streaming water during the winter are further analysed in Fig. 7. In that figure the catch of perch is related to the bottom temperature in the inner part of Hamnefjärden (Fig. 1.) and that of roach to the bottom temperature at the trap. These temperatures should be representative of the conditions for outgoing and ingoing fish. The big catches of both species occur on the same day as or a day after a drop in temperature connected mostly (except in the case of February 18, 1972) with a break in the heating of the cooling water. This indicates that roach is staying outside the trap, prevented by the heat from entering the bay. The behaviour of perch seems to be a stress reaction when the raised temperature drops. This may also explain the large number of outgoing ruffe on February 7, 1972, recorded in Fig. 7. The high figure for emigrating ruffe in streaming water in that month is largely based on this catch.

The migration of *flounder* in both directions seems to be increased by the current during winter and autumn and decreased during summer. The heating has rather small effects. The immigration is in the main negatively affected.

Among cyprinids migrating mainly in rather high temperatures, only silver bream and bleak were caught to any substantial extent. The ingoing *silver bream* were affected differently by the current in different seasons. The number of outgoing silver bream increased in February—April and September—November. In heated water the catches of ingoing fish were bigger in most months; it is a pity, however, that summer observations of this situation are lacking. The emigration is not changed very much by the heating. Before the starting up of the power plant the *bleak* was caught almost exclusively during June—December. The catches in streaming water were bigger the whole year round with the exception of outgoing fish in December. The significant differences mainly relate to "In". The only clear effect of heat is seen in the increased immigration during December—April.

The catches of *smelt* increased markedly after the starting up of the power plant. The catches were concentrated within the cold season (late autumn—early spring). During this period increases were noted for both directions when cold water was pumped. The reactions to the heating seem rather small.

Table 4 and Fig. 6 may be summed up as follows. The current seems to increase the catches of bleak, smelt, silver bream and flounder. The opposite is true for burbot, sea scorpion, eel pout and perch, while the catches of roach and ruffe do not change very much. The reactions are rather similar for both in- and outgoing fish except in the case of silver bream and eel pout, for which the current gives more positive changes in the emigration than in the immigration. The results indicate that the heating decreases the migrations

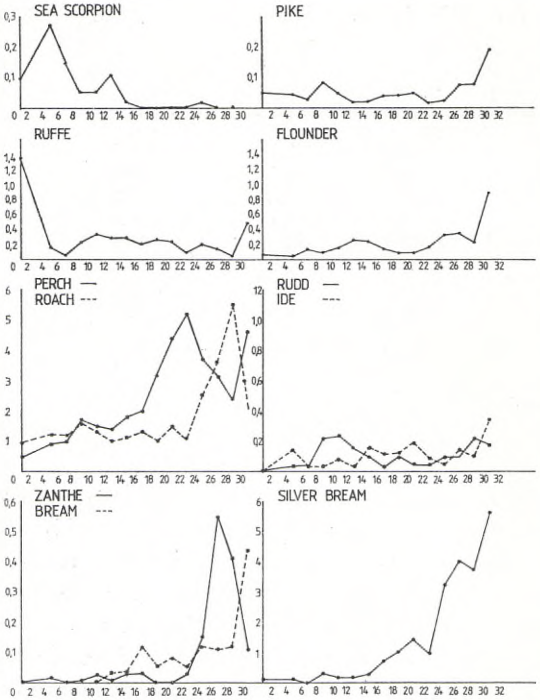

Fig. 8. Catches in the gill nets in relation to the temperature. Number per net per night 2nd half-year 1972—76.

of sea scorpion, eel pout, ruffe, perch and, less markedly, also of roach and ingoing flounder. Positive changes have been noted for the immigration of silver bream and bleak.

The catches in the gill nets

The relationship between catch and temperature was also investigated for the gill nets in Hamnefjärden. The number of fish per net per night within temperature intervals of 2°C was calculated using the temperature at each net at its setting. The second half-year 1972—76 was selected in order to avoid the spawning season of most species and to get as wide a range of temperature as possible. The result is shown in Fig. 8. *Sea scorpion* is mostly caught in low temperatures ($< 14°C$), while the opposite is true for *silver bream*, *bream* and *zanthe* ($> 24°C$). The other common species are more frequently caught in both low and high temperatures, but *flounder*, *perch*, *roach* and *ide* give the best catches in warm water. *Pike* and *ruffe* are rather evenly distributed along the temperature scale, apart from the high value for ruffe in the interval 0—2°C. This peak may be due to stress reactions in connection with interruptions of the heating, as was reported for the migration trap (Fig. 7). The *rudd* shows a peak between 8 and 12°C.

An interesting observation can be made in Fig. 8. For all species except sea scorpion a marked maximum occurs within a narrow interval around 30°C. This cannot represent the temperature preferendum; it is more likely that it is caused by stress due to the abnormally high temperatures. Death in high temperatures has been observed for pike. During four days in August 1975 with temperatures of 31—32°C, 47 dead or dying big pikes, 2—4 kg, were registered in the inner part of Hamnefjärden. The stationary mode of living that is characteristic of pike could have contributed to the deaths. The large size of the observed fishes seems to indicate that big pikes are more vulnerable to heat than are smaller ones. An alternative explanation could be a higher degree of territorial behaviour among big pikes.

The effect of the operating of the station on the catch size has been tested by comparing the mean numbers per night before and after the start of it. The analyses have been made separately for the periods May—June and August—October and for these two periods together. The limitation is governed by the routines before 1970. As can be seen in Table 5, the catches of perch and bream have increased considerably, while the opposite is true for sea scorpion, ruffe and pike. The total numbers of roach, flounder and silver bream have stayed remarkably constant considering the heating of about 5—10°C. The reactions to the heating are further discussed later on.

The mean weights before and after the starting up of the station have been compared for the periods May—June and August—October together. The changes were moderate except for a decrease for silver bream (150—90 g) and an increase for pike (630—1,300 g). So far there has been no satisfactory explanation of these changes. However, seen together with the figures in Table 5, the lower weight of silver bream could indicate a better recruitment and a higher predation on big fish, while the higher weight and smaller number

Table 5. *A comparison between catches 1966—71 and 1972—76.* Mean number/night (18 nets)

	May—June		Aug.—Oct.		Total	
	1966—71	1972—76	1966—71	1972—76	1966—71	1972—76
Sea scorpion	4.5	— 0.6	0.8	0.4	2.4	— 0.5
Ruffe	25.5	— 8.6	5.7	4.2	14.0	— 6.0
Pike	1.6	1.0	1.7	— 0.7	1.6	— 0.8
Flounder	6.3	11.1	5.2	3.6	5.7	6.6
Perch	36.8	+88.2	32.9	+55.6	34.5	+68.6
Roach	51.5	37.0	19.3	31.4	32.7	33.6
Bream	0.3	0.5	0.1	+ 1.5	0.2	+ 1.1
Silver bream	18.4	17.0	17.0	21.1	17.6	19.5

\+ 1972—76 significantly (5 %) bigger than 1966—71.
— 1972—76 significantly (5 %) smaller than 1966—71.

of pike might be caused by a lower recruitment and a better growth. Such changes would probably be most marked for the stationary pike which according to the catches in the migration trap (Table 1) has a low interchange with populations outside Hamnefjärden. Further, relative immobility of the species should lead to it being underestimated in the catches. Thus the number of big pikes with a high consumption of food in the high temperatures could be substantial and their predation an important factor in regulating the populations of the other species.

V. DISCUSSION

Generally speaking, the fish fauna of the Baltic archipelagoes is composed of warm-water fishes, in most cases of freshwater origin, and mainly marine cold-water species. The warm-water species generally occupy shallow and sheltered areas, while the cold-water species predominate at greater depths and in open water in direct contact with the open sea and large firths (Neuman 1974 a and 1977). Thus, as is evident from Table 1, freshwater fish dominate the shallow investigation area. The cold-water species move into that area in the cold season, perhaps partly as a result of low competition from the rather inactive warm-water species. There are, too, observations of freshwater fish in the winter moving to deeper localities with somewhat higher temperatures than the shallow areas (roach, Neuhaus 1936, and bream, Svärdson 1965). Thus the catches presented in this paper partly reflect, especially for the cold-water group, migrations which probably are caused largely by an interplay between temperature preferenda and competition; they do not, however, give any direct information on the preferendum and the temperature of maximum activity. For perch and roach, however, Neuman (1979) has shown that the catches discussed are mainly the results of the level of activity. This is probably also true for the other freshwater fishes with their main distribution in the investigated biotopes.

According to Fry (1971), the amount of energy available for activity reaches its maximum at the temperature preferendum. Assuming that the catches of warm-water fish roughly reflect the level of swimming activity, the temperature of maximum catch still does not necessarily coincide with the experimentally established preferendum. Deviations occur owing to the absence of high temperatures in nature and to a seasonal rhythm of activity giving high activity at low temperatures, especially in connection with spawning. Thus, the catch/temperature relationship reflects both the amount of energy available for activity and the way in which it is distributed amongst different activities.

A summary of the results presented in this paper is made in Table 6, which shows the temperature limits for the maximum catch and the changes in the catch size that are connected with the starting up of the power station. The limits must be regarded as approximate. Big catches

Table 6. *Cold- and warm- water species.*

	Temperature of maximum catch			Changes after the starting up of the station		Lethal temperature
	Migration trap		Gill nets			
	Before start	After start	After start	Trap	Gill nets	
Burbot	< 4	(< 10) *		—		
Sea scorpion	≤ 6	≤ 6	< 8	—	—	24.3—26.0 [1]
Eel pout	< 6	< 6		—		26.6—29.0 [2]
Ruffe	2—10	8—22	8—22	—	—	34.3—34.7 [3]
Pike			8—22		—	30.0—35.1 [4 5]
Perch	4—16	16—20	18—28	—	+	30.0—36.7 [3 4 6]
Roach	2—14	8—24	> 24	—	=	30.0—38.2 [3 4 6]
Flounder	4—10	20—22	12—28	—	=	29.0—34.0 [7]
Bleak	6—10	20—24		+		37.7—40.6 [3]
Rudd	10—14	14—24	8—12			36.5—38.2 [3]
Ide	4—14	20—26	14—22			35.8—38.2 [3 6]
Zanthe	10—16	16—20	> 24			
Bream			> 24		+	30.0—35.7 [4 6]
Silver bream	6—12	> 14	> 24	+	=	

*) Very small catches.
— the catch decreases after the starting up.
+ the catch increases after the starting up.
= the catch do not change after the starting up.

[1] HUNTSMAN and SPARKS 1924.
[2] ALTMAN and DITTMER 1966. (American species, *Macrozoarces americanus.*)
[3] HOROSZEWICZ 1973.
[4] SHKORBATOV 1964.
[5] SCOTT 1964.
[6] HOROSZEWICZ 1966. [Experiments on lethal temperatures (unpublished).]
[7] WAEDE 1954.

considered to reflect spawning activity and stress reactions are excluded.

It would have been interesting to compare the grouping of species in the table and the temperature of maximum catch with experimentally established preferenda. Such information, however, is available for only a few of the species in question. Moreover, the observations have been made in different ways that are difficult to compare. Some reference for the grouping can be taken from the lethal temperatures entered in the table. Unfortunately these, too, suffer from having been established in different ways.

The temperatures of maximum catch in the migration trap are higher since the heating began, except in the case of the cold-water species, which seem to avoid warm water. The higher temperatures for the other species probably reflect the existence of temperatures closer to the preferenda. For gill nets, which have been fished in warmer water, the values are still higher, except in the case of rudd. They may be compared with observations by ALABASTER (1963), who studied selected temperatures in laboratory gradients and in heated rivers. Laboratory data for roach lie between 19.5 and 26.8°C in July and in the field most fish was caught between 21 and 27°C. The laboratory preferendum for bream was found to be 26.5°C (July) and both roach and bream seemed to be attracted by heated effluents. Experiments with perch were made in October—November, giving a final selected temperature of 17.8°C. LENKIEWICZ (1964) gives lower values for bream (10.5—20.6°C). She also found low preferenda for ide (9.9—23.7°C). This probably reflects low acclimatization temperatures. For the American perch, *Perca flavescens*, laboratory data vary between 20.0 and 29.0°C (MCCAULEY and READ 1973, BARANS and TUBB 1973, MCCAULEY 1977) and field observations between 19.7 and 21.2°C (FERGUSON 1958).

In the presentation of the gill-net catches high catches — for most species the highest catches —

were noted in temperatures around 30°C. This probably reflects stress reactions to temperatures approaching the lethal level (see Table 6). Normally the temperature seldom exceeds 20°C in a bay like Hamnefjärden. It is noteworthy that rather large amounts of fish appear to remain in very high temperatures, in the case of pike even at the lethal level. This could be explained by the location of the discharge point (Fig. 1) preventing escape from the inner part of Hamnefjärden by forming a "thermal barrier". HOROSZEWICZ (1973) states that roach, rudd and perch in heated lakes avoid temperatures exceeding 28.0—28.5°C.

In Table 6 the changes in the catches after the starting up of the power plant can be related to the temperatures of maximum catch. The decrease of burbot, sea scorpion and eel pout and the increase of immigrating silver bream and bleak are in agreement with the catch/temperature relationship. Surprising decreases were noted, however, for ruffe, perch and, less markedly, also for roach and flounder at temperatures below those for maximum catch in heated water. As regards ingoing fish, this must to a great extent be due to the special hydrographic conditions around the trap. This is sited on a sill three metres deep between Hamnefjärden and the sea. The countercurrent under the cooling water does not reach the sill but meets the warm water just outside it. Here a strong thermocline — 8—9°C in about two metres — develops. Fish approaching the trap from the sea swimming under the heated water, will thus have to force this gradient before being caught. With this in mind it is hardly surprising that the catches of bottom fishes such as the cold-water species and ruffe[1], perch and flounder decrease when the station is operating. The cyprinids are more vertically dispersed (NEUMAN 1974 a) and consequently not so drastically affected. It is likely, however, that a negative effect of the "thermal barrier" is seen in the decrease of roach and the limited increase of silver bream. Except in the case of the cold-water species, the heating should increase the emigration owing to higher activity. The absence of such an effect could reflect an attraction to the heated water within Hamnefjärden and, in the case of ruffe, perch, roach and flounder, it could also reflect the decreased immigration.

The changes in the catches in the gill nets in Hamnefjärden after the starting up of the power plant (Table 5) correspond to what could be expected from the temperatures of maximum catch as regards the decreases in sea scorpion, ruffe and pike, and the increases in perch and bream. The sea scorpion probably leaves the bay, while the comparatively high catches of ruffe and pike in high temperatures rule out the idea that avoidance is the only responsible factor. The marked decrease in ruffe during May—June indicates a disturbance of the spawning activity. This could mean a lower recruitment, which cannot be compensated for by the reduced immigration. As was mentioned under "Results" the higher mean weight and smaller catch of pike indicate reproduction disturbances, which will affect this seemingly isolated stock rather soon. A lower activity above the temperature preferendum might also explain part of the decrease in catches of ruffe and pike.

The more or less unchanged catches of flounder in the heated bay could be the result of a balance between decreased immigration and higher activity. The increase in perch probably reflects higher activity; it is not likely that the stock had grown very much in spite of the drastically reduced immigration in both streaming and heated water. The low figures for roach in heated water during spring in both the gill nets and the trap indicate a negative effect on the spawning activity, which should affect the recruitment. The catches of bream in the trap were small, but they have increased since the starting up of the station (NEUMAN 1974 b). Thus, a bigger immigration together with a rise in the activity can explain the bigger catches in the nets. The constant figures for silver bream, a warm-water species,

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[1] NYMAN (1975) has found differences between the gene frequencies of ingoing and outgoing ruffe in heated water. He considers that the ingoing fish are "attracted" by the hot water owing to their genetic character. Considering the big decrease of the immigration in heated water, NYMAN's interpretation means that within the same species there is a minority attracted by the steep gradient described above, while the majority are repelled. I consider it more probable that the gradient is an obstacle to all ruffes, though of course less so to those that enter the trap.

are surprising in view of the somewhat increased immigration and the good catches in high temperatures. The absence of an increase, together with the lower mean weight noted above (p 101), could be interpreted as the result of a heavier predation pressure from pike and perch. The high temperature must increase the consumption substantially. Generally, the predation must be considered an important factor masking the direct effects of the heating in this comparatively isolated recipient. The fishing in Hamnefjärden may be compared with corresponding studies made in heated lakes in Poland (FRIÉSKE 1970), which have many species in common with Hamnefjärden. No major changes in the average biomass of fish were noted, but the catches of bream and silver bream increased.

Analysing the catches in the migration trap, it is evident that for most species the current has a stronger effect than the heating. It is noteworthy that most species react positively or negatively to the current irrespective of their direction of migration. The observations of increased emigration are not congruent with FRY's observation (1958) that fish has a tendency to resist being swept downstream. Perhaps the current is too weak — it is seldom more than 0.5 m/sec at the trap — to evoke this reaction. The rather low velocity cannot to any considerable degree prevent the larger fish from entering the trap; during one minute fairly fusiform fish can swim about 10 x 1/sec (l=length of body) (BAINBRIDGE 1958). The increase in the catches of the plankton-feeding bleak and smelt may partly be due to the transport of food with the current.

VI. SUMMARY

The relationship between catch and temperature was investigated for the fish fauna at a cooling water outlet in the Baltic. The fishing was carried out with a trap blocking the passage between the sea and the bay into which the heated water is discharged, and with gill nets within this bay. The investigation was conducted both under natural conditions and in heated water.

On the basis of the temperature of maximum catch the common species are grouped as follows:

Low temperatures: Burbot, sea scorpion and eel pout.
Even distribution in medium temperatures: Ruffe and pike.
Medium and high temperatures: Perch, roach, flounder, bleak and rudd.
High temperatures: Ide, zanthe, bream and silver bream.

In the bay, high catches, assumed to reflect stress, were noted for several species around 30°C. The changes in the catches during heating correspond roughly to the grouping above. Deviating reactions are related to special hydrographic conditions at the trap and to presumed changes of the population densities in the bay. The catches in the trap were found to be affected more by the current (0.5 m/sec.) than by the heating.

VII. ACKNOWLEDGMENTS

The investigation was planned together with Professor ULF GRIMÅS and Mr ALLAN ÖSTERMAN. The latter and Mr BIRGER WISTRÖM did most of the fishing. The analysis of the material was discussed with Dr THOROLF LINDSTRÖM and Professor ULF GRIMÅS. Mr LARS NORLING, Miss GUNILLA CARLZÉN, Mr GUNNAR THORESSON and Mr HANS WILLNER carried out the data-processing and the statistical work. The manuscript was discussed with Dr MATS OLSSON. I wish to express my deep gratitude to all these individuals and also to the Oskarshamn Power Group, the National Swedish Environment Protection Board and IBM, Sweden for financing the work.

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Activity of Perch, *Perca fluviatilis* L., and Roach, *Rutilus rutilus* (L.), in a Baltic Bay, with Special Reference to Temperature

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CONTENTS

I. INTRODUCTION

At the nuclear power plants in Sweden, there are in progress extensive fishery biological investigations which have as their main aim that of estimating the effects of heated effluents on the catchability of fish. An important part of these investigations consists of regular test fishings with gill nets and fyke nets carried out over a period of several years before and after the start of the stations. The catch in such a stationary tool is dependent on the number of fish of catchable size in its vicinity, their swimming activity and their reactions to the tool. Analysing catches of fairly stationary species the present author (NEUMAN 1974 a) arrived at the conclusion that the observed large seasonal and daily fluctuations in the catches mainly reflected variations in activity. This conclusion led to the initiation of a description of catches in terms of activity and an attempt to correlate activity to temperature and season, two factors which many authors have found to influence activity. The best material available for this approach was test fishings in a cooling water recipient on the Baltic coast, in which the natural correlation between temperature and season is broken. Perch, *Perca fluviatilis* L., and roach *Rutilus rutilus* (L.), which dominate the catches in the vicinity of the cooling water outlet, were chosen for the analysis presented in this paper.

The indirect way of studying activity by catches in stationary tools has been used in several investigations on yellow perch, *Perca flavescens* (MITCHILL.) The method has been adopted for European perch by TENHUNEN and LIND (1973) and CRAIG (1977), and for both perch and roach by STOTT (1970) and ANDERSSON *et al.* (1972). Field studies of the activity of perch have also been made by direct methods such as sonar (HERGENRADER and HASLER 1967) and television (SIEGMUND and WOLFF 1973).

II. MATERIAL AND METHODS

The investigation was carried out at a nuclear power plant, Oskarshamnsverket at Simpevarp, situated on the Baltic coast of Sweden 220 km south of Stockholm. The first unit was put into operation at the beginning of 1972 and a second one in the autumn of 1974. The total electric power produced is 1040 mW, requiring 50 m^3 cooling water per second, heated 8—12°C. The water is discharged at the southern shore of the bay Hamnefjärden (Fig. 1). The only connection between this bay and the sea is Hamnehålet, which debouches on to an open stretch of coast. The temperature reduction of the cooling water

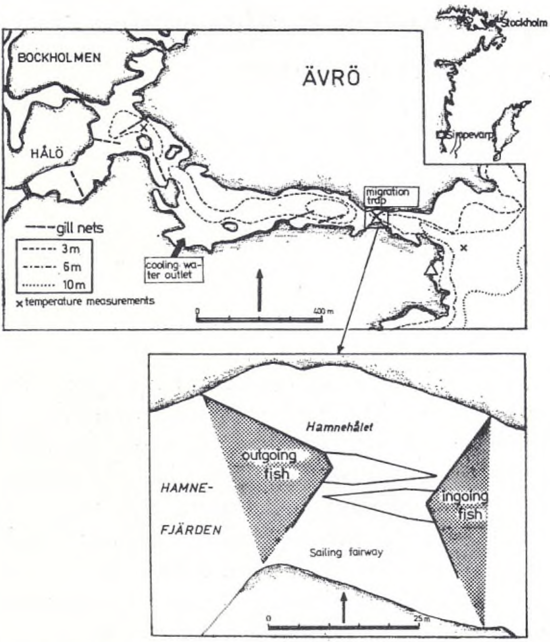

Fig. 1. Map of the Hamnefjärden study area with the location of the traps.

between the outlet and Hamnehålet is insignificant. Inside the point of discharge, however, the currents are very weak, and the water is gradually cooled to only a few degrees above the ambient temperature in the innermost parts of the bay. Most of the bay is between two and five metres deep. The salinity is normally a little above 7 ‰.

The fish fauna in the area has been described by NEUMAN (1974 b). Hamnefjärden is dominated by perch and roach and other limnic fishes. These species spawn in the bay, which also serves as spawning ground for the adjacent open coast. Outside Hamnefjärden, limnic fish are common close to the shore, but further out marine species such as herring, *Clupea harengus* L., and cod, *Gadus morhua* (L.), predominate.

The activity of perch and roach was studied by means of a trap blocking Hamnehålet and of gill nets in Hamnefjärden. The trap consisted of two pound nets placed on a sill three metres deep in the inner part of Hamnehålet (Fig. 1). One net caught fish migrating into Hamnefjärden, the other fish leaving the bay. The mesh size was 28 mm in the arms and 12 mm at the end of the fyke net. The trap was emptied once a day from Monday to Friday inclusive. The fish was registered as to species, direction of migration and length group with a class width of 5 cm (total length), after which it was released in its migratory direction. During part of the summer season a sailing fairway was kept open through the trap, thus enabling some of the fish to pass through unregistered. In connection with the emptying of the trap the temperature was measured at the surface and at the bottom close to the nets and at one locality in the inner part of Hamnefjärden and one outside Hamnehålet (Fig. 1).

The fishing in Hamnefjärden was carried out with 18 bottom gill nets with six different mesh sizes between 21 and 60 mm. The nets had a length of 30 metres and, in the water, a height of about 1.5 m (6-foot nets). They were always placed at the same stations. They were set between 3 and 5 p.m. and lifted between 8 and 9 a.m. the following day. Numbers and total weight of fish were noted for each species and net. The catches were coupled to temperature measurements. Before 1972 only the surface temperature at one point in Hamnefjärden was measured at the lifting of the nets. After that the bottom temperature at each net was registered both at setting and lifting.

The trap was operated for three years beginning in July 1970. Some interruptions occurred, especially in 1971. As far as the gill-net fishing is concerned, this paper treats only periods with one fishing each week, *i.e.* May—December 1970 and the entire period 1972—76.

During the autumn of 1970 and the spring of 1971 part of the catch of perch and roach in the migration trap was marked with Carlin tags. In all 1094 perch and 621 roach were marked.

The investigation area, the operation of the power plant and the methods, especially the migration trap, are described in greater detail in another paper in this publication (NEUMAN 1979).

III. RESULTS

The results are treated below in four main sections. In the first the use of the catches presented in this paper as a measure of activity is discussed. The second section treats the daily fluctuations in

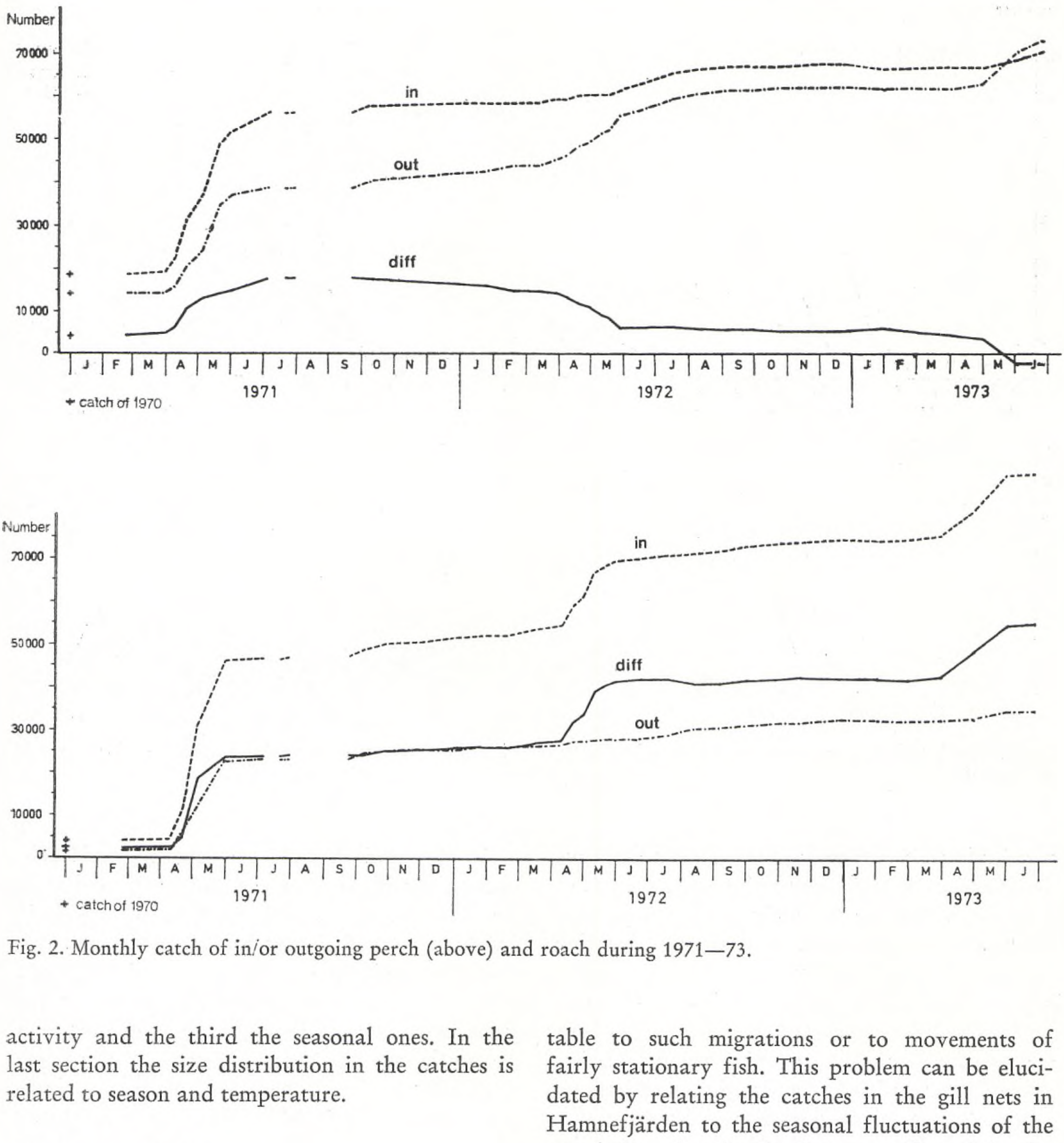

Fig. 2. Monthly catch of in/or outgoing perch (above) and roach during 1971—73.

activity and the third the seasonal ones. In the last section the size distribution in the catches is related to season and temperature.

Catch and activity

As mentioned above, the catch in a net or a trap is dependent both on the density and the activity of the fish around the tool. Migrations between different areas must, within years, be more important for the density in question than is the interplay between recruitment and mortality. As regards the interpretation of the catches, the basic problem is whether they are mainly attributable to such migrations or to movements of fairly stationary fish. This problem can be elucidated by relating the catches in the gill nets in Hamnefjärden to the seasonal fluctuations of the population size in the bay as reflected in the balance between in- and outgoing fish in the migration trap, and by studying the short-term variations in the catches in that tool.

The accumulated numbers of in- and outgoing perch and roach caught daily during the period January 1971—June 1973 in the migration trap and the differences between these values have been calculated and are presented in Fig. 2. In 1970 the perch immigration was of the same order of

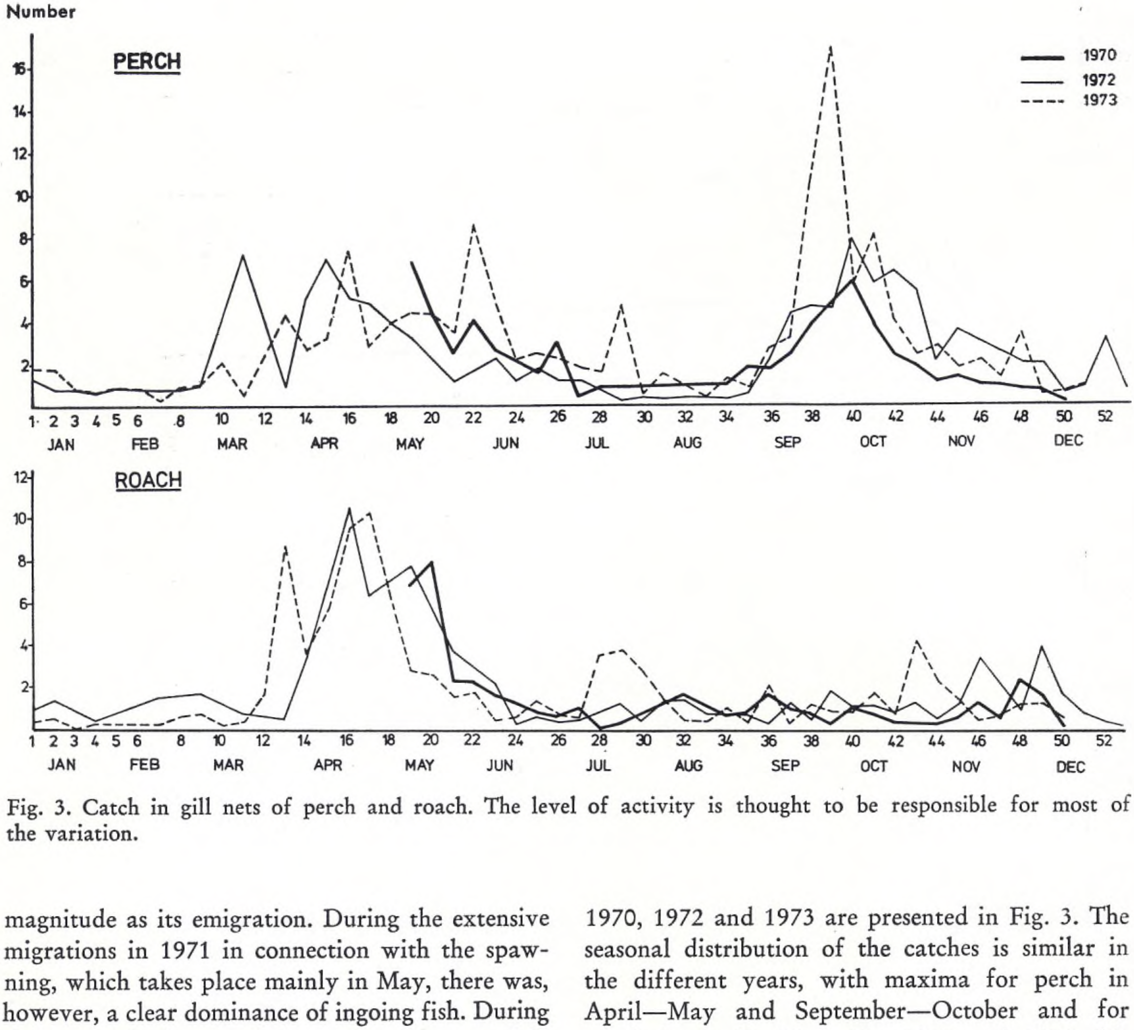

Fig. 3. Catch in gill nets of perch and roach. The level of activity is thought to be responsible for most of the variation.

magnitude as its emigration. During the extensive migrations in 1971 in connection with the spawning, which takes place mainly in May, there was, however, a clear dominance of ingoing fish. During the rest of the year the movements roughly balanced each other. At the beginning of 1972, the power plant was started. This was reflected in smaller catches and an inversion of the relation between immigration and emigration in the spring.

In 1971, the migrations of roach were also concentrated in the period before and during the spawning, *i.e.* April and May. The dominance of ingoing fish was more accentuated than it was in the case of perch. Moreover, owing to the drastic reduction of the emigration, this dominance remained after the starting up of the station, in spite of decreased immigration. The reactions upon the current and the heating reflected in the catches in the trap are treated in greater detail in another paper (Neuman 1979).

The catches in the gill nets in Hamnefjärden 1970, 1972 and 1973 are presented in Fig. 3. The seasonal distribution of the catches is similar in the different years, with maxima for perch in April—May and September—October and for roach in April—May. For 1972 and 1973 this pattern can be compared with the changes in the population reflected in Fig. 2. It is evident that the perch maxima and the decline of the roach catch after the spring peak are not due to migrations through Hamnehålet. As there is no reason to believe that recruitment and mortality could explain the seasonal rhythm illustrated in Fig. 3, variations in the level of activity remain as the most plausible explanation.

The daily catches in the migration trap during July 1970—June 1971 are shown in Fig. 4. The Monday values, representing as they do the catch of three days, have been halved. This operation is based on a comparison between catches on Mondays and on other days during the period July 1970—June 1971. On average the Monday

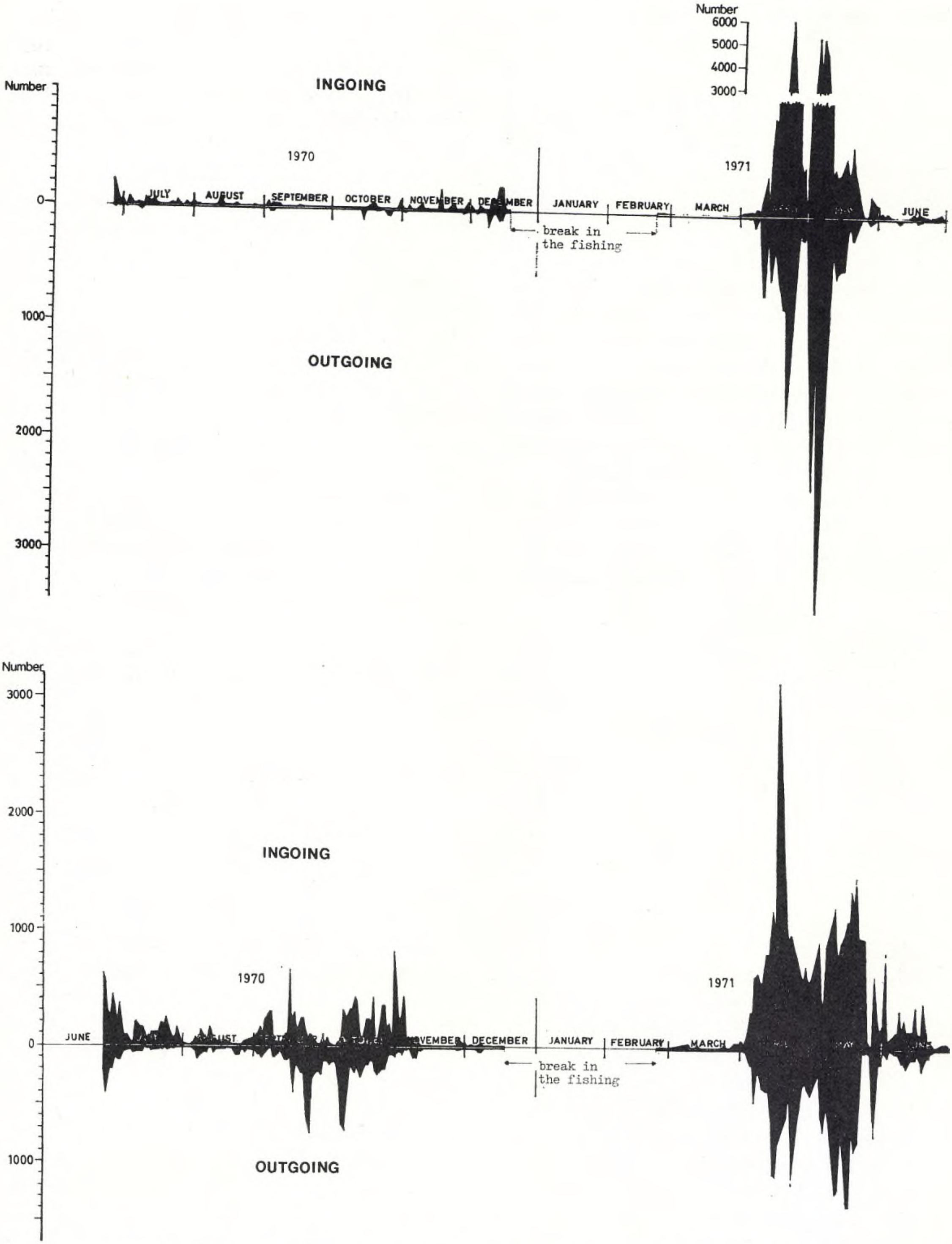

Fig. 4. Daily trap-catches of perch (above) and roach during 1970 and 1971. Note the tendency of covariation between immigration and emigration in the very same day.

Table 1. *The effect on catch of the sailing fairway.*

	Ingoing			Outgoing		
	Monday	Friday	Tuesday	Monday	Friday	Tuesday
Perch	50	55	67	45	77	56
Roach	25	32	32	17	39	38

catches were approximately twice as big as the others (NEUMAN 1974 a). As can be seen, the yields not only of the net catching fish leaving Hamnefjärden but also of the net depending on populations outside the trap shows the same seasonal pattern as the catches in the gill nets. This supports the hypothesis that activity and not migrations between different areas is the main factor.

Other characteristics of Fig. 4 are the big daily variations and a tendency towards covariation between immigration and emigration in the same day. This tendency has been statistically established for perch during spring and summer and for roach during spring (see next section). The large short-term fluctuations are probably caused by changes in the level of activity and not by migrations between different areas. The same thing applies to the simultaneity of the variations in the catches in the two directions; this must be due to the fact that the swimming activity changes at the same time on both sides of the trap.

The relation between catch and activity might be disturbed not only by migrations between different areas but also by avoidance of the tools. Thus it is probable that the proportion of fish avoiding the tackle varies according to the light conditions. This should especially be true with regard to the gill nets, which presuppose "invisibility". Consequently, it is possible that the low catches during summer are partly due to avoidance. It should be noted, however, that the catches of perch, at any rate, are rather good in June. In the case of this species, the catches might be influenced by the annual light cycle for the further reason that perch is mainly day-active (ANDERSSON *et al.* 1972, SIEGMUND and WOLFF 1973, TENHUNEN and LIND 1973, and ERIKSSON 1978). The gill nets are fished from 3—5 p.m. to 8—9 a.m. and so mostly cover the dark part of the 24 hours. Thus the estimation of the activity during late autumn and winter may be too low. However, the catches are also very low in the continuously fishing migration trap. The problem in question should not affect the roach, which is mainly night-active (ANDERSSON *et al.* 1972).

Under "Material and Methods" above it was mentioned that a sailing fairway was kept open south of the migration trap during the summer (Fig. 1). The effect of this on the catches has been analysed on the basis of the catches in 1972, when the fairway was open only during weekends. The mean values of the catches on Mondays, Fridays and Tuesdays are given in Table 1. The Monday values have been halved to make them comparable (see above, p. 110).

Although the Monday catches are of course lower than the others, especially as regards outgoing roach, the decrease is not big enough to cast doubt upon the classification of the summer activity as low. That classification is supported by the low catches in the gill nets.

Thanks to the simultaneous fishing with the gill nets and the trap, it seems possible to conclude that the daily and seasonal variations in catches mainly reflect fluctuations in the swimming activity of fairly stationary fish.

Daily variations in activity

The daily variations in the numbers of in- and outgoing fish in the migration trap have been related to each other and to the temperature. Correlation coefficients measuring the correspondence in the direction and amplitude of the changes in the time series have been calculated in pairs (KENDALL 1976). The possibility that a catch in one direction is related to a catch in the other direction or to the temperature one or a few days earlier has been examined by displacing the series in relation to each other by up to five days ("cross correlation"). The analyses have been made separately for different periods in 1970—71. The division into periods has been made on the basis of the catch curves in Fig. 4 according to the principle that each period should include a fairly large number of observations and that it should have a mean level of catch distinct from those of the adjoining periods. The time periods and the

Table 2. *The correlation between catches of in- and outgoing fish. Only correlations significant at the 5 %/o level are shown. Coefficients based on < 5 observations are excluded.*

(a) Perch

	July 1—Aug. 28, 1970			Aug. 31—Nov. 4, 1970			Nov. 5—Dec. 19, 1970		
Time difference, days	Number of observations	Ingoing related to outgoing n days earlier r	Outgoing related to ingoing n days earlier r	Number of observations	In after out	Out after in	Number of observations	In after out	Out after in
5	15	—	—	18	no significant coefficients		11	no significant coefficients	0.85
4	8	—	—	9			6		—
3	8	—	—	9			5		—
2	16	0.84	—	18			10		—
1	24	0.60	—	28			16		0.75
0	34	0.43	0.43	38			24		—
	Feb. 22—March 26, 1971			March 29—April 16, 1971			April 19—June 2, 1971		
5	(3)	no significant coefficients	no significant coefficients	(4)	—	—	11	—	—
4	(2)			(2)	—	—	5	—	—
3	(4)			(3)	—	—	5	—	—
2	7			6	0.96	0.88	11	0.64	0.56
1	10			9	0.83	0.92	18	0.56	0.57
0	15			12	0.68	0.68	25	0.56	0.56
	June 3—July 29, 1971			Sep. 21—Dec. 30, 1971					
5	9	—	—	13	no significant coefficients	—			
4	(4)	—	—	5		—			
3	(4)	—	—	8		0.84			
2	9	—	0.66	16		0.74			
1	15	0.81	0.60	24		—			
0	22	0.80	0.80	42		—			

(b) Roach

	July 1—Aug. 28, 1970			Aug. 31—Nov. 4, 1970			Nov. 5—Dec. 19, 1970		
Time difference, days	Number of observations	Ingoing related to outgoing n days earlier r	Outgoing related to ingoing n days earlier r	Number of observations	In after out	Out after in	Numbers of observations	In after out	Out after in
5	15	0.63	—	18	—	no significant coefficients	12	no significant coefficients	—
4	8	—	—	9	—		7		—
3	8	—	—	9	—		7		0.88
2	16	—	0.58	18	—		13		0.94
1	24	—	—	28	0.47		20		0.73
0	34	—	—	38	—		27		—
	Feb. 22—March 26, 1971			Mar. 29—June 2, 1971					
5	(3)	no significant coefficients		17	—	—			
4	(2)			8	—	—			
3	(4)			8	0.99	0.97			
2	7			17	0.95	0.78			
1	10			27	0.85	0.75			
0	15			37	0.89	—			
	June 3—July 29, 1971			Sep. 21—Dec. 30, 1971					
5	9	no significant coefficients		26	—	—			
4	(4)			13	—	—			
3	(4)			13	—	—			
2	9			27	—	—			
1	16			42	0.86	0.46			
0	22			57	—	—			

Table 3. *Recaptures in Hamnehålet.*

	Number marked	Recaptures in the other migration direction within one month	
		number	per cent
Perch, autumn			
Marked as ingoing	106	3	2.8
„ „ outgoing	193	24	12.4
Perch, spring			
Marked as ingoing	379	17	4.5
„ „ outgoing	416	29	7.0
Roach, autumn			
Marked as ingoing	256	14	5.5
„ „ outgoing	82	3	3.7
Roach, spring			
Marked as ingoing	146	3	2.1
„ „ outgoing	137	6	4.4

significant correlations between catches in the two directions are shown in Table 2. The correlation with the temperature is treated later on.

Table 2 shows "in-out" correlations on the same day for perch during spring and summer and for roach during spring. These correlations during the spawning season, when there is a strong predominance of ingoing fish, are of especial interest in this context. During this period it could be expected that a directed migration to the spawning places in Hamnefjärden would be succeeded by a migration out of the bay after the spawning. A simultaneity of movements in and out was also observed in corresponding studies in 1969 and 1970 at Marviken, an archipelago area 130 km north of Simpevarp (Neuman 1974 a). In addition to perch and roach this phenomenon was also observed for silver bream, *Blicca bjoerkna* (L.), rudd, *Scardinius erythrophtalmus* (L.), and ruffe, *Gymnocephalus cernua* (L.).

The balance between in- and outgoing fish during most of the year (Figs. 2 and 4) shows that long-lasting "one-way" movements did not take place. According to the results of the cross correlation, however, a movement in one direction was quite often followed by a movement in the other direction one or a few days later. This was the case with perch during spring and summer and with roach during spring and late autumn. The irregular pattern of these correlations makes it difficult to give them a biological interpretation. Possible explanations of the correlations between catches with a time difference between them are that the same fish may have returned the next day or some days later or that other fish may have responded to stimuli, such as changes of temperature, that reached the fish on the two sides of the net with a certain time lag. A prerequisite for resolving this problem would have been extensive marking. The marking carried out gave very few recaptures in the other direction of migration (Table 3). But this result should not be taken too seriously, in view of the facts that only a small proportion of the catch was marked and that the effect on the fish of the marking has not been tested.

For 1970—71, the cross correlation technique has also been used to analyse the relation between the catch and the temperature at the tool the same day and up to five days earlier. The results are presented in Table 4. Only a few significant coefficients can be established, most of them concerning perch. With one exception they are all positive. Most of the correlations relate to late autumn, but the parallel increase of catch and temperature at the beginning of April is also reflected in the table. Cross correlations between the number of ingoing perch and the change of temperature from day to day have been made without giving any significant correlations. The results of the analyses were too meagre to justify further statistical attempts.

Seasonal variations in activity

Marked seasonal variations in activity are evident in the catches both in the gill nets (Fig. 3) and in

Table 4. *Correlations between catch and temperature.*

The number of days between temperature observation and catch are given for the significant (5 ‰) correlations. They are all positive except the one marked (—). (The number of observations is shown in Table 2.)

	Perch		Roach	
	In	Out	In	Out
1970				
July 1—Aug. 28				
Aug. 31—Nov. 4	0 (—)		2, 3	
Nov. 5—Dec. 19	2, 3	2		
1971				
Feb. 22—March 26				
March 29—April 16	0, 2	0, 1, 2		
April 19—June 2		3		
June 3—July 29				
Sep. 21—Dec. 30	0, 5	0, 1, 2, 3, 4	3	4

the trap (Fig. 4). The perch has maxima in the spring and at the beginning of the autumn and minima in the summer and the winter. The roach shows high peaks in April and May and rather small catches during the rest of the year. Fig. 3 shows that these patterns remain more or less unchanged after the starting up of the power station and the accompanying heating. This stability is further illustrated by Fig. 5, where catches and temperatures are compared for 1970, the best investigated year before the start, and 1976, when at least one of the two units and usually both were in operation. As can be seen, the seasonal patterns are similar in the two years but the levels are higher in 1976, at least for perch.

The stability of the seasonal variations in the gill net catches has been further analysed by time-series technique (Kendall 1976) for the period 1972—76. For that purpose the years were divided into 25 "seasons" of two weeks each, weeks 51 and 52 being excluded. On this material it was investigated whether there was any significant increase or decrease of catch from 1972 to 1976. It has been found that this was not the case, the periodicity was described by means of autocorrelations for different intervals of time between the "seasons". For a specific interval the correlation coefficient was calculated for all possible pairs of observations, *e.g.* for interval 1 (two weeks) x_1x_2, x_2x_3, x_3x_4, etc. (x_1 = season 1) and for interval 25 (one year) x_1x_{26}, x_2x_{27}, etc. The result is shown in Table 5.

As regards perch, the similar coefficients for intervals 1 and 25 and the higher values for intervals 24 and 26 as compared with interval 2 show a strong annual periodicity. This is still more pronounced for roach, where the coefficient for interval 25 is higher than that for interval 1.

Although the annual rhythm of activity seems to be independent of the often widely

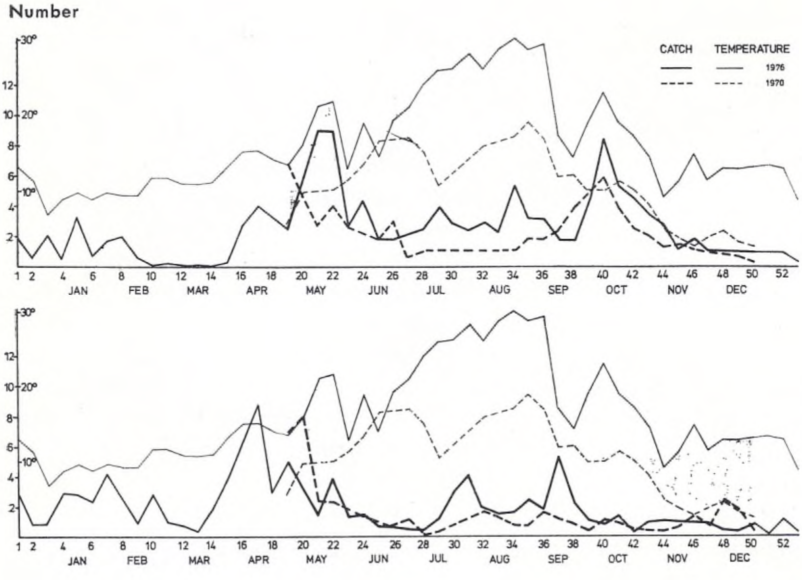

Fig. 5. Catch of perch (above) and roach in 1970 and 1976 compared to the water temperature. The seasonal patterns are similar but catch levels are higher, at least for perch, when the nuclear plant was producing heated effluent water.

Table 5. *The periodicity of the catches.*

Intervals (number of "seasons")			Correlation coefficients	
			Perch	Roach
2 weeks	1		0.62	0.57
	2		0.29	0.18
	3	The highest positive coefficient between intervals 3 and 22 is 0.10 for perch; for roach all are negative.	0.02	—0.08
	22		—0.09	—0.05
	23		0.15	0.18
	24		0.44	0.51
1 year	25		0.58	0.67
	26		0.47	0.54
	27		0.29	0.15
	28		0.05	—0.11

fluctuating temperatures, Fig. 5 indicates that, within seasons, the level of activity is influenced. This possibility was statistically tested for the period 1972—76. First, two sign tests were made on the whole catch in Hamnefjärden and the mean temperature of all nets at the setting. The first test eliminated the seasonal variation by comparing, for each week, the signs of the deviations of catches and temperature from the mean for that week during the years 1972—76. For the whole year a significant (1 %-level) positive correlation was found for perch. This result is due to weeks 17—41 (end of April—middle of October), while there are no significant correlations during the rest of the year. A positive correlation (1 %) was found for roach, too, during the summer season, weeks 20—36, but for the winter and spring, weeks 1—19, there exists a negative correlation (5 %). The second sign test eliminated disturbances from possible long-term variations by comparing the direction of the changes of catch and temperature between consecutive weeks. In this case, the combination of signs is rather similar between seasons, and consequently the year has not been divided. There is a positive correlation (1 %) for perch but not for roach.

The relation between catch and temperature in different seasons during 1972—76 was further investigated by means of a rank correlation (*ad mod.* KENDALL 1948) and a regression analysis. The ranking was done on the means of catch and temperature for all nets each week. In the regression analysis the difference between each catch in a separate net and the mean for that net and week in the period 1972—76 were correlated with the corresponding difference for the temperature at the setting. In this case the four nets with 50 and 60 mm mesh size were excluded because of the very low catches in them. The correlations are presented in Table 6. Both analyses were made for different periods formed on the basis of the catch curves (Figs. 3 and 5). The period of low catches in late autumn and winter was divided into two parts around the midwinter solstice. Beginning in March there is a period with increasing catches up to and including the spring maximum. For perch the next period is formed by the decrease after the spawning and the summer minimum, after which there follows the peak in early autumn. For roach the decline after the spring maximum has been separated from the

Table 6. *The correlation between gill-net catches and temperature.*

		Rank correlation		Regression	
	Week	n	r	n	r
Perch	53—11	50	—0.09	722	0.08
	12—21	46	0.33 [1]	658	0.22 [1]
	22—35	68	0.17	952	0.31 [1]
	36—43	40	0.48 [1]	560	0.37 [1]
	44—52	42	0.37 [1]	576	0.19 [1]
Roach	53—12	56	0.01	778	0.07
	13—17	25	0.25	350	0.01
	18—22	22	—0.11	308	—0.15
	23—32	49	0.38 [1]	686	0.30 [1]
	33—40	40	—0.06	560	—0.07
	41—52	57	0.08	786	0.08

[1] significant at the 1 % level.

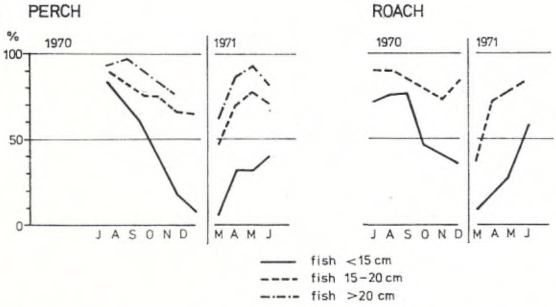

Fig. 6. The percentages of fish caught in different sizes as a monthly average (*cf.* text).

summer minimum. The next period is constituted by the rather good catches from the middle of August to the beginning of October.

As is evident from Table 6, the results of the two analyses agree rather well. The catch of perch is positively correlated to the temperature during the whole year except for the period from the end of December to the middle of March. For roach the only correlations significant at the 1 % level relate to the summer minimum, June to the middle of August. The negative coefficients for May could indicate that a change in the normal relation between temperature and season disturbs the spawning.

To sum up, the fishing in Hamnefjärden shows that the activity is governed mainly by a seasonal rhythm and not by the temperature level. If the seasonal dependence is eliminated, however, positive correlations between catch and temperature can be established. The seasonal dependence is emphasized by the absence of such correlations in the winter. This indicates that the low catches are not caused simply by low temperatures. The activity of perch seems to be more sensitive to temperature variations than is that of roach.

The influence of season and temperature on the length distribution

In the preceding sections the number of fish caught was related to season and temperature. In the present section the influence of these two factors on the size distribution of the catches in the migration trap is examined. This is done on the basis of the registration in length groups (total length) with a class width of 5 cm. Most of the analyses concern the share of the total catch represented by fish shorter than 15 cm; 10—15 cm is the shortest length group caught without any considerable selectivity of size. First, the monthly values for the percentage of small fish were calculated for the period July—December 1970 and March—June 1971 (see Fig. 6), *i.e.* before the starting up of the power plant. The corresponding calculation was also performed for bigger fish. In doing this, the influence of fish shorter than 15 cm on the percentage shares was eliminated by relating fish 15—20 cm in length only to fish longer than 15 cm. For perch, the percentage of all fish longer than 20 cm accounted for by fish measuring 20—25 cm was also calculated. In- and outgoing fish were treated together.

Fig. 6 shows marked seasonal differences in the length distribution. The percentage of perch shorter than 15 cm is at its highest (83 %) in July 1970 and then decreases every month to a minimum in the winter (7 % in December 1970 and 6 % in March 1971). It increases in the spring of 1971 to 40 % in June. The curves for bigger fish show the same tendency; the greater flatness of these curves and the higher percentages represented by them are probably attributable to the small share of the biggest fish. For roach the maximum percentage of small fish is more extended (71 % in July—75 % in September) than for perch and the decrease during the autumn is slower. In the spring there is a rise from 9 % in March to 59 % in June. The curve for fish 15—20 cm in length is similar, except for a rise from November to December.

When looking for the cause for the observed seasonal changes of the length distribution, it is natural to consider the temperature. The intermittent heating of the water — up to 10°C at the trap — during 1972 and 1973 which breaks the natural temperature/season relationship offers an opportunity to separate the influence of these factors. The operation of the station was very irregular in the months January—April 1972, and after the beginning of May there was a complete break until September. From September production was almost continuous, until the middle of April 1973, after which there was no heating until the end of June. The fishing was stopped after that month. The percentage of fish shorter than 15 cm in the different catch years is shown in Fig. 7. The share of small perch is bigger during most of the time when the station is in operation, *i.e.* winter and autumn. For roach the proportion of small fish is larger during the winter and the spring, while the difference is insignificant in the autumn. Thus it seems clear that the temperature influences the length distribution.

The influence of temperature, season and operation of the plant on the length distribution were further analysed by statistical means. This was done by a regression analysis with the bottom temperature at the trap, the day number (1—365) and heating/no heating as the independent variables, and the quotient between number of fish shorter than 15 cm and total number each day as the dependent variable. In- and outgoing fish were considered both together and separately. In order to make the analysis of the day number meaningful, the different half-years were studied separately. The second half of 1971 was excluded owing to long breaks in the fishing. The results of the analyses are presented in Table 7.

The information in Table 7 may be summed up as follows. During 1970—71 the correlation coefficients relating to in+out and in and out separately are very similar and are significant for both temperature and day number. This orderly pattern is broken when the plant starts; the significant correlations are fewer and in some cases, especially in 1973, the sign of significant day number coefficients is shifted, probably owing to a break in the heating during most of the period April—June. In contrast, the significant coefficients for temperature and heating are all positive. This indicates that the good correlation for the day number in 1970—71 was due to temperature more than to any other factor correlated to the season. During 1972—73, however, the correlations between the proportion of small fish and the temperature are mainly confined to the second half of 1972. This is probably due to the drastic reductions of the natural migrations caused by current and heating, especially during the spawning period (Neuman 1979).

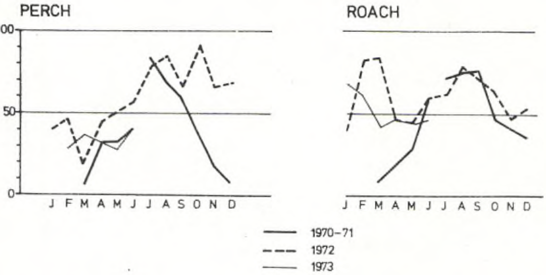

Fig. 7. The percentage of fish shorter than 15 cm in monthly catches during the years 1970—73 (*cf.* text).

In order to illustrate the catch/temperature relationship and the differences between small and big fish (limit 15 cm) in this respect, the catches of ingoing perch have been related to the temperature of the sea just off Hamnehålet. In Fig. 8 the numbers of small and big perch are presented together with the temperature at 4—5 m depth each day. During July and August 1970, both the total catch and the catch of big perch are mainly low and the temperature is high. During the period September 10—15 the relationship between small and big perch changes drastically in connection with the relatively much greater increase in the catch of big perch. At the same time the temperature falls from 13° to 8°C. Similar changes occur in the period October 7—9, 23—26 and October 29—November 5. In the spring of 1971 the share of small fish increases from a low winter level during the first increase of catch and temperature at the beginning of April. The next big change takes place during May 24—27, when the temperature rises markedly and the catch of, in particular, large perch decreases rapidly.

On the whole small and big perch exhibit concurrent changes in the catches. The large perch, however, show a greater variability, and a higher activity in low temperatures. The changes in the length distribution are not smooth, but take place by leaps as a result primarily of fluctuations in the behaviour of the big fish. This often happens in connection with rapid changes of temperature, a circumstance which indicates a higher sensitivity to temperature in big fish.

Changes in the length distribution in the catches similar to those in Hamnehålet were also observed at Marviken during May and June 1970. The number of fish exceeding 15 cm in length decreases for perch, roach and rudd at the end of the spawning. The opposite is the case with small fish.

Table 7. *The correlation*[1] *between length distribution (quotient ⩽ 15 cm/total catch) and day number, temperature and heating.*

		Before start		After start		
		July—Dec. 1970	March—June 1971	Jan.—June 1972	July—Dec. 1972	Jan.—June 1973
Perch Number of observations						
	In+out	119	82	113	108	96
	In	116	82	102	98	63
	Out	116	74	111	95	96
Day number						
	In+out	—0.85***	0.78***	0.14	—0.10	—0.31**
	In	—0.81***	0.69***	0.20*	—0.08	—0.17
	Out	—0.77***	0.69***	0.09	0.23*	—0.36***
Temperature						
	In+out	0.57***	0.75***	0.16	0.34***	0.10
	In	0.54***	0.66***	0.17	0.07	0.22
	Out	0.57***	0.64***	0.03	0.28**	0.03
Heating						
	In+out	—	—	0.04	0.02	0.26**
	In	—	—	—0.01	—0.03	0.34***
	Out	—	—	—0.02	0.37***	0.26**
Roach Number of observations						
	In+out	122	80	113	125	123
	In	116	78	108	117	117
	Out	105	72	108	121	111
Day number						
	In+out	—0.59***	0.73***	0.00	—0.23**	—0.24**
	In	—0.53***	0.72***	—0.03	—0.36***	—0.10
	Out	—0.41***	0.56***	0.00	—0.16	—0.20*
Temperature						
	In+out	0.53***	0.74***	—0.11	0.35***	0.06
	In	0.53***	0.76***	0.02	0.39***	0.03
	Out	0.21*	0.55***	—0.13	0.29***	0.05
Heating						
	In+out	—	—	0.02	0.06	0.17
	In	—	—	0.10	—0.06	0.04
	Out	—	—	0.08	0.06	0.17

The trend is similar, at least for perch, in the spawning bays and in an exposed locality in an adjacent firth, which indicates that the change is not due to migrations between different biotopes (Neuman 1974 a).

IV. DISCUSSION

The possibility of using the catches presented in this paper for studying activity was discussed above (p. 109). It was concluded that the variations in catch were mostly due to variations in activity, but that avoidance of the tools may lead to an underestimation of the summer activity.

The movements registered in the catches could have the character of regular seasonal or daily migrations between different biotopes or undirected, more or less "random" and spontaneous movements. Seasonal migrations of perch have been observed by many authors, among them Allen (1935) and Worthington (1949) for Lake Windermere in England; for the Baltic less marked

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[1] Levels of significance: ***—0.1, **—1, *—5 %.

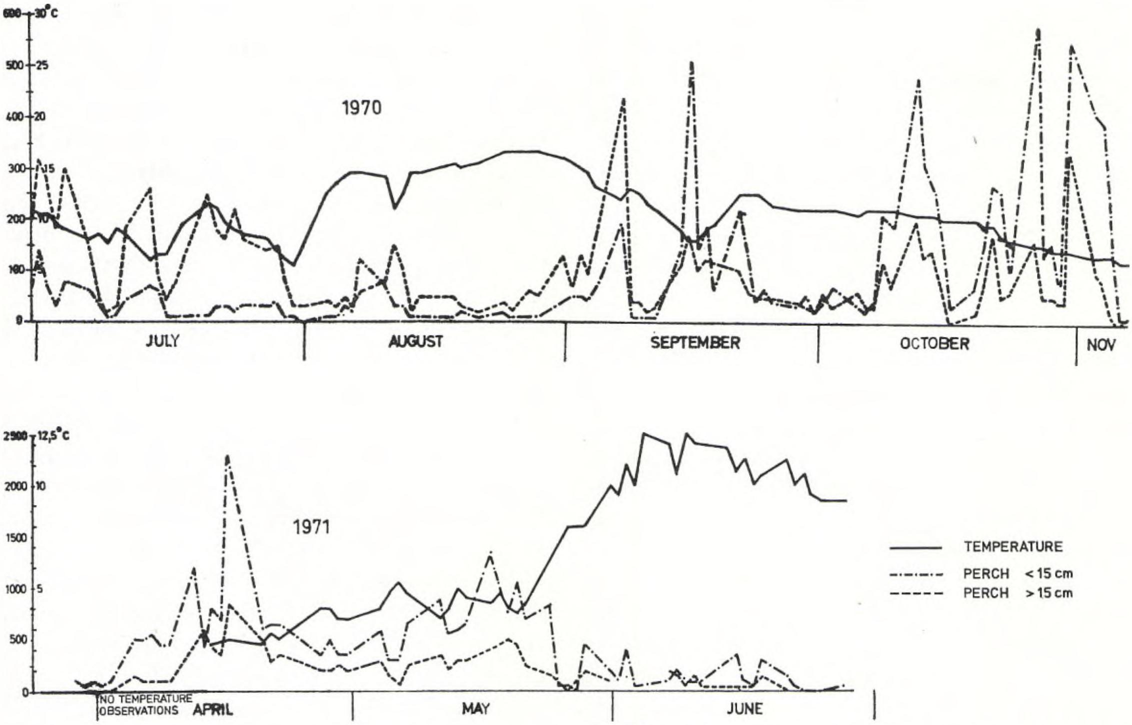

Fig. 8. The relation between water temperature and catch of perch, larger or shorter than 15 cm. On the whole larger perch are more active in low temperature.

migrations have been observed by Henking (1923) and Neuman (1974 b). Earlier in this paper (p. 110), however, it was shown that in the case of Hamnefjärden such movements do not affect the catches significantly, except possibly in the spring. Scott (1955) and Hasler and Bardach (1949), among others, have shown a daily migration between shallow water at night and deeper water during the day. The fact that only a very small proportion of the perch in Hamnefjärden was caught in the migration trap each day indicates that there is no strong tendency towards a daily migration between Hamnefjärden and the sea. Within the small and rather uniform Hamnefjärden it would be difficult to distinguish this form of activity from a more or less undirected one.

A further study of the catches in the migration trap before the starting up of the power station supports the idea that the movements of perch and roach have a mainly undirected and "random" character. It has been established that the catches of in- and outgoing fish on the same day are correlated during the spring and, in the case of the perch, also in the summer. A covariation between a movement in one direction and a movement in the other direction occuring one or a few days later has also been found for parts of the year. This means that fish in Hamnefjärden, with its sheltered and limnic character and higher temperature, and fish at the exposed marine coast outside the bay shift location at the same time or with a short time lag. The correlations between the migration directions are especially interesting in the case of the spring, when there is a dominance of incoming fish before and during the spawning time. Thus the concentration at the spawning places seems to take place by more or less random movements. This could occur if the fish moved around less when they had found favourable places. In the spawning season similar patterns of catch have also been observed in other localities and for other species (Neuman 1974 a). If there is a tendency for homing, as has been claimed for perch (Worthington 1949 and Agnedal 1968, among others), my hypothesis means that the homing relates to a rather big area and not to the specific spawning place.

Several investigations have been made into the influence of season and temperature on the activity of perch. In tank experiments at the Arctic circle, Eriksson (1978) found that the level of activity was correlated to temperature and the duration of activity to day length. However, he observed a higher level of activity in June than in the warmer month of July, and he mentions the possibility that this could be caused by the physiological state of the fish at the spawning, which in the north normally takes place in June. This hypothesis is supported by Siegmund and Wolff (1973), who observed an extra peak of activity occurring between the usual ones in the morning and afternoon during the spawning time, May. Fishing perch with small traps and gill nets close to the Arctic circle in the summer, Tenhunen and Lind (1973) noted a significant correlation between the number of active hours per day and the temperature. These results, however, are difficult to compare with other investigations owing to the short duration of all seasons except winter at this latitude. On the basis of gillnet catches in Lake Windermere in England, Craig (1977) found that the activity of perch was positively correlated to the temperature and that the daily duration of activity was restricted by a high light intensity. Hergenrader and Hasler (1967) studied the swimming speed of yellow perch during different seasons by following the fish with sonar. They found low values in the winter and a maximum in July and August and a linear relationship between the speed and the temperature within the range tested (0—22°C). No observations were made between March 8 and May 25; this period includes the high activity around the spawning.

Regarding perch, the results presented in this paper deviate from those reported above by the high amplitude of the activity peaks before and during the spawning and the peak at the beginning of the autumn. It is reasonable to suppose that in a laboratory study the activity around the spawning will be underestimated owing to the lack of adequate stimuli from other fishes and from the environment, *e.g.* the spawning places. The surprisingly low catches during the summer may be connected with the annual condition cycle. For adult perch in Lake Windermere in England, LeCren (1951) found that the minimum of condition occurred just after the spawning and the maximum in September. Probably the amount of energy available for swimming is lower in the summer than in September, which could explain the pattern of catch. It may be noted that Neuman (1976) states that the perch in the Simpevarp area grows best in September. As mentioned earlier (p. 112), the low summer catches may be partly due to avoidance of the tools. A similar but less marked seasonal pattern of catches in gill nets during May—October has been shown for a great number of stations representing different biotopes at the Baltic coast, including the Simpevarp area (Neuman 1974 b).

The sparseness of literature on the activity of the roach makes it difficult to discuss this topic. However, much of the picture outlined above for the perch may also be valid for the roach. The fact that the correlations between catch and temperature are confined to the summer indicates that the latter species is less sensitive to temperature variations than is the perch. The same tendency was observed in the extensive gill-net fishing mentioned above (Neuman 1974 b). Positive catch/temperature correlations were established for the perch during August—October, while the correlations for the roach were weaker and were mainly confined to August.

Among the factors regulating the share of the available energy — the "scope for activity" (Fry 1947) — which is used for swimming, could be seasonal differences in the choice of food and in the behaviour of the food organisms. Preliminary results from studies of the food of perch in Hamnefjärden indicate that crustaceans dominate in the summer, while small fish become the most important food for adult perch in September and remain so during the rest of the autumn (Karås, pers. comm.). The rise of activity in September could partly be the result of a change to more mobile food. The absence of a corresponding peak of activity in the autumn for roach supports this idea; the roach do not prey on fish.

The low summer catches of both species and the fact that the seasonal rhythm of activity seems to be uninfluenced by the heating argue against a simple, direct relationship between activity and temperature. The probable non-existence of such a relationship is also indicated by the absence of positive correlations between catch and temperature in the winter; the activity stays low independently of the temperature. It seems probable that the catch/temperature correlations reflect an influence on the variations in swimming speed and/or the duration of swimming activity between days and weeks, but that the basic level for longer periods is regulated by other factors, *e.g.* the light conditions, the condition cycle and the choice of food. In other words, the temperature dependence of the swimming activity is to a great extent overshadowed by seasonal variations in the scope for activity and its distribution between different activities.

Although the daily and seasonal variations of the catches in the migration trap are mostly similar for fishes of different size, the size distribution in the catches is strongly influenced by the temperature. The big fish seem to be comparatively more active in low temperatures and their behaviour to be more affected by thermal changes. FERGUSON (1958) states that for yellow perch and several other species the temperature preferenda for small fish are higher than for bigger ones. In gill-net catches, MALONEY (1969) observed a decline of yellow perch bigger than 22.5 cm from May to August, whereas the catch of smaller perch remained fairly constant throughout the season. He suggested that the large perch had either moved out of the netting areas or had become markedly less active than the smaller fish. SCOTT (1955) noted that perch longer than 25 cm did not occur in a shallow and presumably warm bay of Lake Erie during the summer. Similar observations have been made for other species, *inter alia* by FRY (1937) and KENNEDY (1941). The size distribution in the catches in the migration trap could hardly have been dependent to any great extent on migrations to and from Hamnefjärden, since a balance between immigration and emigration existed for both small and big fish during almost the whole year.

The low proportion — below 10 % — of perch and roach shorter than 15 cm in the winter can hardly reflect their share of the population. The discrepancy may partly be due to the fact that to swim the necessary distance to be caught, the small fish have to make more swimming movements than the big ones and consequently use a larger part of the scope for activity. This could be important in a season when the condition is low (LECREN 1951), and the temperature far below the optimal. Probably the proportion of fish longer than 15 cm of the population is underestimated in the catches in high temperatures. As was mentioned above, the big fish seem to have lower temperature preferenda than the smaller ones and to be more sensitive to thermal changes. URSIN (1963), BRETT (1970) and others point out that with increasing size the balance between anabolic and catabolic processes becomes less favourable. LECREN (1958) and NEUMAN (1976) have shown that for perch the year-to-year variations of growth and their dependence on temperature increase with size. This must mean that the metabolism becomes more controlled by the temperature. For the big fish, the importance of the catabolism is accentuated by the spawning, which prolongs the time for restoring the condition after the winter. Thus, LECREN (1951) established that, while adult perch reach their maximum of condition in September, for immature ones this occurs already in August. In analogy with this, mature perch seem to grow best in September and immature ones in August in the archipelagoes discussed here (NEUMAN 1976).

It is reasonable to presume that the temperature preferendum is lowered when the condition is low and significant amounts of energy are needed for feeding. BRETT (1971) has experimentally established a temperature preferendum of about 15°C for *Oncorhyncus nerka* (WALBAUM) given food in surplus. In nature, however, this species moves from the warm epilimnion to a hypolimnion of about 5°C for digesting the food, because it is best used at this low temperature. JAVAID and ANDERSON (1967) found that starvation influenced the temperature preferred by three salmonids; it decreased for two species but increased for the third.

Thus, the observed size-dependent differences in the activity/temperature relationship may be caused by the magnitude of the scope for activity influencing the temperature preferendum and the activity response to temperature. The way in which the scope is distributed between different activities may also be affected by the choice of food. As was mentioned above, big perch feed mainly on crustaceans in the summer but in the autumn they feed largely on fish, which probably requires a higher activity, while the small perch keep to invertebrates all the year round.

V. SUMMARY

The seasonal and daily variations in the swimming activity of perch and roach were studied by fishing with stationary tools. The work was carried out in a Baltic bay which receives heated water from a power station. Gill nets were set once a week in the bay, and a trap enabling registration of in- and outgoing fish to be made daily blocked the passage between the bay and the open sea outside. In this paper are presented gill-net catches for one year before the starting up of the power plant and five years after it; the migration trap was in operation one year and a half before the starting up and for the same period after it.

On the basis of a comparison between the simultaneous catches in the gill nets and the trap, it was concluded that the daily and seasonal variations in the catches mainly reflected fluctuations in the activity level and not migrations between different areas. Before the heating began, it was established that for some seasons a movement from the bay was correlated to a movement into it the same day or a few days later, and *vice versa.* This indicates an undirected and "random" character of the movements. This pattern is especially typical before and during the spawning time, when there is a dominance for fish moving in towards the spawning places in the bay.

The gill-net catches show an annual rhythm of activity, uninfluenced by the heating, with maxima in the spring and, for perch, also at the beginning of the autumn. Comparing the same week in different years, positive correlations have been found between catch and temperature; for perch these relate to the whole year except the winter, for roach only to the summer. Probably these correlations reflect an influence of temperature on the variations in swimming activity between days and weeks, while the basic level for longer periods is regulated by other factors. These factors have not been studied in this investigation, but the influence of the seasonal variations in the condition, the spawning, the light conditions and the choice of food is discussed.

Under natural conditions the proportion of perch and roach shorter than 15 cm in the migration trap exceeded 70 % in the summer but did not reach 10 % in the winter. Thanks to the artificial heating it was possible to show that the temperature and not the season is the regulating factor. It is suggested that the low proportion of small fish at low temperatures is partly due to a lower swimming performance. The big fish seem to be more sensitive to changes of temperature and to have lower preferenda, attributes which may be connected with the relationship between metabolism and size.

VI. ACKNOWLEDGMENTS

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Food and Habitat of the Fish Community of the Offshore Region of Lake Vänern, Sweden

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CONTENTS

I. INTRODUCTION

Lake Vänern is the largest lake in Sweden, and the third largest in all Europe (5,650 km^2). Table 1 shows the general characteristics of Vänern as compared with the three other great lakes of Sweden.

As can be seen from the table, Vänern is an oligotrophic lake with a mean depth of 27 m. The fish community of this large lake is, of course, of great interest (Table 2). It reflects the normal fauna of a southern Swedish lake, except for the presence of landlocked salmon, which occurs as two separate populations in the lake (*vide infra*).

Also of special interest is the hydrology of the lake, characterized as it is by water movements resembling ocean currents. Fig. 1 (from HOLMSTRÖM and CARLSSON 1978) shows clearly the presence of "anticlockwise" currents both in the main body of water of Vänern (Värmlandssjön and in the smaller part, Dalbosjön). As a consequence of these currents a warmer watermass and a concentration of nourishment characterize the western shore of the main lake (Värmlandsnäs and the archipelago of Lurö) (Fig. 2).

The material here presented was collected during the years 1972—74, partly by the use of sinking gill nets, partly by trawling with the research vessel THETIS.

Material collected in June 1975 and analysed by APPELBERG (1977) is also partly included in this paper. The investigation is intended as a case study, with a view to forming a basis for comparisons with future research. The offshore fish community has been chosen in this paper because of its relatively simple structure as compared with the littoral communities, which, however, have also been subjected to intense sampling (*cf.* ALMER 1978).

II. MATERIAL AND METHODS

All material was collected at fixed stations as shown in the map, Fig. 2. The test-fishing with

Table 1. *Morphometrical and hydrological data (from National Swedish Environment Protection Board 1975).*

	Vänern	Vättern	Mälaren	Hjälmaren
Surface area km^2	5,650	1,912	1,140	484
Precipitation area km^2	46,830	6,359	22,603	4,053
Maximum depth m	106	128	61	20
Mean depth m	27	39	13	6.1
Water volume km^3	152	74	14	3
Mean water supply m^3 sec—m^3 sec	544	42	168	27
Mean discharge 1 sec · km^2—1 sec · km^2	11.6	6.6	7.4	6.6
Retention time, years	8.8	58	2.8	3.7
Characteristic physico-chemical and biological data, 1972—73				
Secchi disc transparency m	4.0	10.0	3.5	2.2
pH	7.1	7.6	7.5	7.5
Total N mg/l	0.70	0.50	0.75	0.71
Total P mg/l	0.008	0.005	0.038	0.044
20°C-Conductivity 20°C mS/m	8.0	11.0	17.0	19.0
α-Chlorophyll α mg/m^3	2	1	11	26

Table 2. *Fish species of Lake Vänern, (r=rare, +=sparse, ++=not common, +++=common, ++++=very common).*

Salmon, *Salmo salar* L.	+
Brown trout, *Salmo trutta* L.	+
Whitefish, *Coregonus* spp. (5 species)	++++
Cisco, *Coregonus albula* (L.)	++++
Smelt, *Osmerus eperlanus* (L.)	++++
Grayling, *Thymallus* thymallus (L.)	r
Pike, *Esox lucius* L.	+++
Roach, *Rutilus rutilus* (L.)	++++
Dace, *Leuciscus leuciscus* (L.)	++
Ide, *Leuciscus idus* (L.)	+
Chub, *Leuciscus cephalus* (L.)	++
Minnow, *Phoxinus phoxinus* (L.)	+
Rudd, *Scardinius erythrophthalmus* (L.)	++
Asp, *Aspius aspius* (L.)	+
Tench, *Tinca tinca* (L.)	++
Bleak, *Alburnus alburnus* (L.)	+++
Silver bream, *Blicca bjoerkna* (L.)	+++
Bream, *Abramis brama* (L.)	++++
Zope, *Abramis ballerus* (L.)	++
Zanthe, *Vimba vimba* (L.)	++
Crucian carp, *Carassius carassius* (L.)	+
Carp, *Cyprinus carpio* (L.)	r
Spined loach, *Cobitis taenia* L.	++
Eel, *Anguilla anguilla* (L.)	++
Burbot, *Lota lota* (L.)	++++
Perch, *Perca fluviatilis* L.	++++
Sander, *Stizostedion lucioperca* (L.)	+++
Ruffe, *Gymnocephalus cernua* (L.)	++++
Sculpin, *Cottus gobio* L.	+++
Four-horn Sculpin, *Oncocottus quadricornis* (L.)	r
Three-spined stickleback, *Gasterosteus aculeatus* L.	+++
Ten-spined stickleback, *Pungitius pungitius* L.	++

so-called survey nets (sinking gill-nets with a specific set of mesh sizes) was carried out in connection with stations set by the National Swedish Environment Protection Board, which was in charge of the strictly limnological survey of the lake during July and August 1973. The trawling (with a floated trawl) was carried on in connection with the fixed stations in August 1972 and in the first half of September 1973, and in June 1975. The trawl was hauled for about 30 minutes at different depths (0—10, 10—20, 20—35, and 35—45 m) at a speed of 3.0 knots. The vertical opening of the trawl was then about 10 m.

From the catches were taken sub-samples, which were analysed at the Institute of Freshwater Research, Drottningholm (about 3,000 stomach samples to date). Identification of the different food items was carried out so far as this was possible. On the other hand, the frequency of the items was estimated according to a subjective scale (+, ++, +++, etc.).

APPELBERG (1977) also included in his material plankton samples analysed by B. GRÖNBERG. For further data on zooplankton, see GRÖNBERG (1976). More detailed data (mainly tables) as to the present investigation were published by NILSSON (1974).

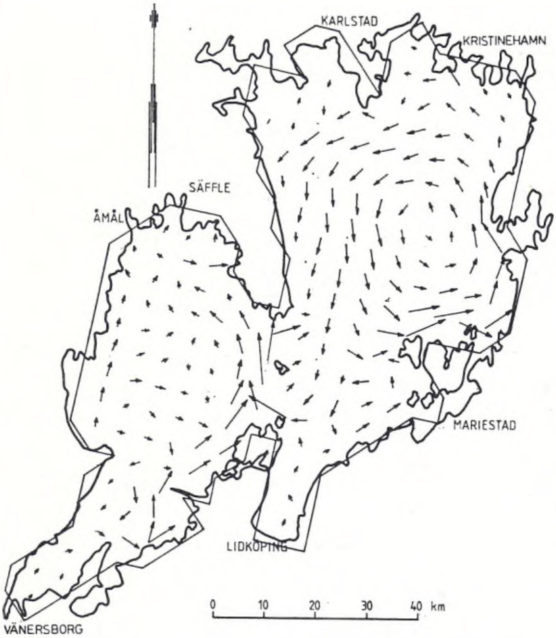

Fig. 1. The water currents of Lake Vänern, 0—10 m, September 1971. (From Holmström and Carlsson 1978.)

III. THE PELAGIC FISH

Migrations

It is a well-known fact that most pelagic species of fish display some sort of diel migrations (for a summary, see Northcote 1967, 1978). According to Brett (1971) this is an adaptation for saving energy by feeding in the upper parts of the waters at dusk and then migrating down to colder water to digest the food in a temperature zone which is optimal for the species in question.

According to Almer and Larsson (1974) and Almer (1978) the cisco (*Coregonus albula*) accumulate in summer during daytime at a depth of 10—13 m. At dusk the school rises towards the surface of the water and it breaks up, after which the fish "rain" down to deeper water and, at the same time, move away from the shallow water close to the shore. The fish then accumulate at a depth of 10—18 m. At dawn the fish again move closer to the shore and school at a depth of 10—13 m.

In the autumn similar migrations occur, though at that time of the year the schools accumulate at greater depths. Echosoundings in September 1973 at station 8 (see map, Fig. 2) during daytime (2.30—3.30 p.m.) and at dusk (8—10 p.m.) (Fig. 3), showed that during daytime the fish (mainly cisco) accumulated in dense schools at a depth of about 35 m. This accumalation of fish is, however, dispersed at dusk and a concentration in the surface layers of the water can be observed.

The general diel migration pattern here described is, however, greatly complicated by the fact that the fish also display vast horizontal migrations. Tagging experiments have, for instance, demonstrated that cisco migrate between Värmlandssjön and Dalbosjön (Enderlein 1977). At other times the middle of the lake (Fig. 2, station 3) is nearly empty of pelagic fish, these having migrated towards the western shore areas. Table 3 shows the catches of cisco from 30-minute trawl hauls at the middle station 8 and the shore station 13 in May 1974.

The factors releasing such migrations are still unknown. However, it can readily be imagined

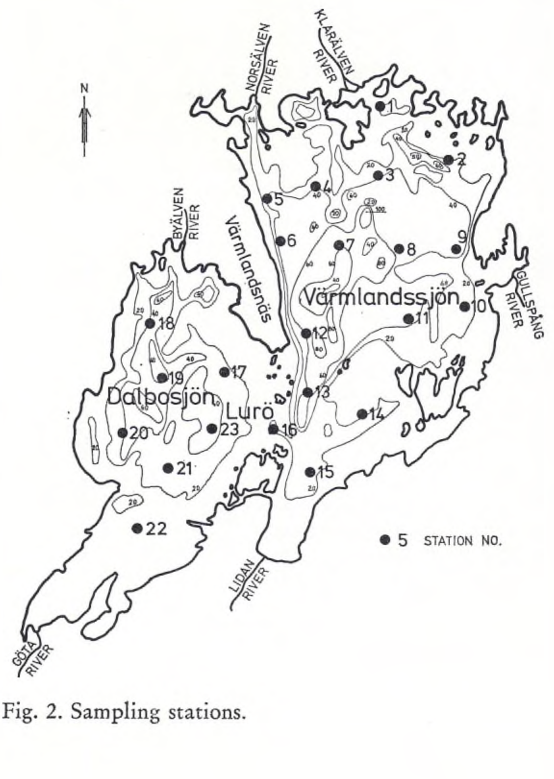

Fig. 2. Sampling stations.

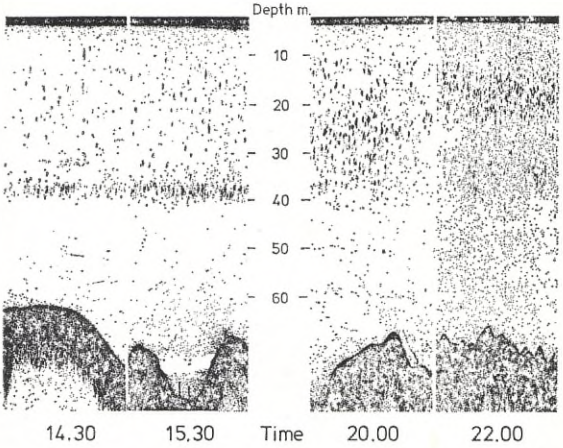

Fig. 3. Echograms showing the diel migration of fish (mainly cisco and smelt) at Station 8.

that the "anticlockwise currents" in combination with favourable winds could give rise to dense concentrations of food, especially along the western shores (Värmlandsnäs and the archipelago of Lurö).

The cisco-smelt relation

Svärdson (1966) listed the occurrence of cisco and smelt (*Osmerus eperlanus*) in 110 lakes in northern Sweden. He found that cisco occurred in 71 of these lakes and smelt in 51, but that only in 13 of all 110 lakes did the two species occur together. Svärdson concluded that this was a result of competition, which meant that the two species can live sympatrically only under special circumstances. In three of the great lakes of Sweden both species occur together (Vänern, Vättern and Mälaren), but in Hjälmaren only smelt is present.

In lakes where the two species live sympatrically one would expect some sort of niche diversification, for example through differences in habitat or food selection.

Table 3. *Vertical distribution of cisco at a pelagic station (8) and a shore station (13),* May 1974.

Depth	Station 8	Station 13
0—10 m	1	≃ 6,000
10—20 m	24	751
20—35 m	42	163

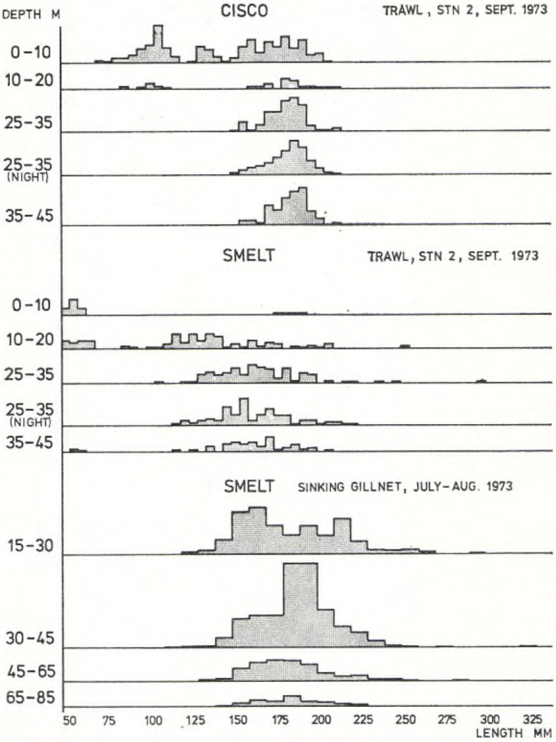

Fig. 4. The vertical distribution of cisco and smelt caught with trawl, and smelt caught with gill net. Bars indicate number of fish caught.

Fig. 4 gives some evidence for a habitat segregation in Lake Vänern. During daytime in the autumn only a few smelt were caught at a depth of 0—10 m, whereas the catch data for cisco was as high as 554. During spring the segregation is still more pronounced (see Table 4).

There is a considerable vertical overlap between the two species, but it is obvious that on the whole smelt are more bound to deeper water (*cf.* also Appelberg 1977).

Table 4. *Number of smelt and cisco caught at different depths,* May 1974.

Depth	Smelt	Cisco	Number of hauls
0—10 m	3	1,388	6
10—20 m	23	547	6
20—35 m	123	70	3

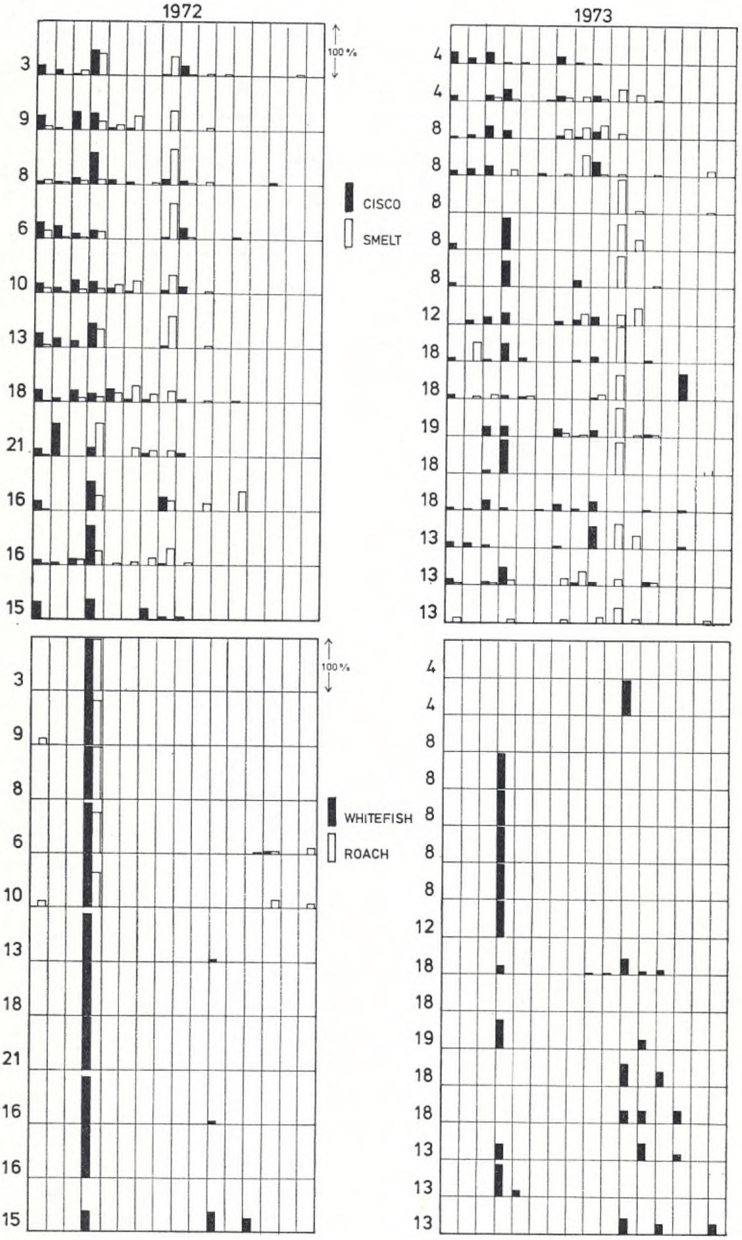

Fig. 5. The food of smelt, cisco, whitefish and roach, caught with trawl in August 1972 and September 1973.

These observations are in agreement with earlier findings from other lakes (*cf.* Rosén 1955, Andersson 1968, Northcote and Rundberg 1971).

It is also clear from Fig. 4 that there is, in addition, a certain size segregation, the smallest specimens of cisco as well of smelt having been caught in the upper layers of the water (down to 20 m), the largest specimens at a great depth.

Food habits

Representative food samples were obtained from smelt, cisco, whitefish (*Coregonus* spp.) and roach (*Rutilus rutilus*). The results of the analyses are presented diagramatically in Figs. 5—6. A special sampling was carried out on salmon (and some trout) caught by the commercial fishermen all over the lake. Unfortunately no distinction between salmon and trout could be carried out in that connection.

It is obvious from the diagrams that geographically there exist certain differences in the diet of the fish. Still more obvious, however, is the fact that some food items always predominate irrespective of the part of the lake in which the fish have been caught. This may reflect the tendency of the pelagic fish to be highly mobile, and possibly also indicates a homogeneity of the pelagic zone as a whole.

The differences between years may be due to differences in the time of year, as well as yearly fluctuations in the availability and sizes of the prey species populations.

Below some characteristics of the different pelagic species of fish are given.

Salmon

There are in Lake Vänern two subpopulations of landlocked salmon, which do not seem to interbreed. These are: the "Klarälven salmon", which spends 3 years in the River Klarälven and returns for spawning after 3—4 years, and the "Gullspångsälven salmon", which spends 2 years in the River Gullspångsälven and returns after 4—5 years in the lake (Runnström 1940). The growth rates of the two populations are strikingly different. Tagging experiments with reared smolt have shown that after 40 months in the lake the salmon from Gullspångsälven attain a weight of about 5 kg, whereas the salmon from Klarälven reach only 2.5 kg (Wickström 1974). They are also segregated spatially during their life in the lake, the majority of the "Gullspångsälven salmon" having been recaptured in the southern part of Dalbosjön, the "Klarälven salmon" elsewhere (Wickström 1974). This should indicate an inherent capacity for niche diversification between the two stocks.

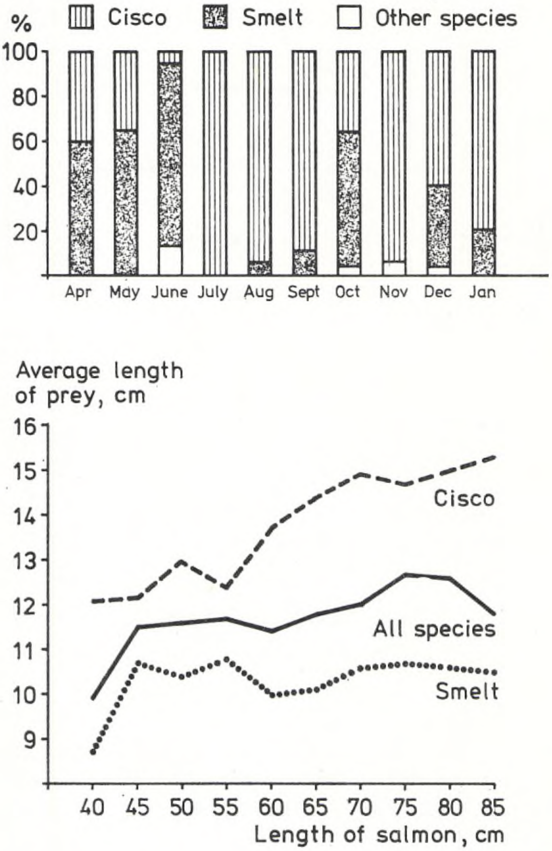

Fig. 6. The food of salmon (and some brown trout) in Vänern, April 1975—January 1976. The seasonal fluctuations in the consumption of smelt, cisco and other species (above), and the relation between the size of salmon and its prey (below).

The food habits of the salmon (both stocks and also including some brown trout) are illustrated in Fig. 6. It is obvious that cisco and smelt play by far the most important role in the diet of the salmon throughout the year although a certain seasonal variation in the relative importance of the two species can be discerned. This mainly

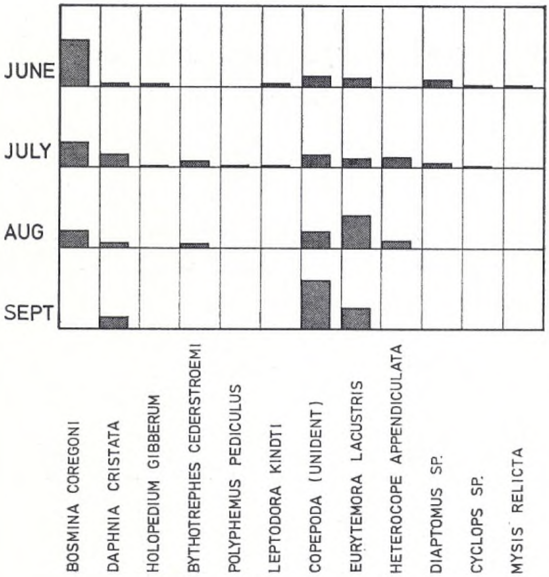

Fig. 7. Seasonal fluctuations in the food habits of cisco caught in the Lurö archipelago, June—September 1973.

means that smelt are available as food for salmon during seasons when they dwell in relatively shallow water during spring and late autumn, while cisco are predominant as food during summer and winter.

Fig. 6 also illustrates the general trend for bigger fish to feed on bigger prey (cisco), or to feed on prey of an optimal size (smelt). Other fish species caught by the salmon were whitefish, roach, stickleback and perch.

Cisco

The cisco feed in the autumn mainly on *Cladocera*, especially the large species *Bythotrephes cederstroemi*, but also prey on copepods, *e.g. Eurytemora lacustris* and *Diaptomus lacustris* (Fig. 5).

Fig. 7 shows that there is a certain seasonal variation in the food habits of the cisco (the samples were taken from fish caught in trap nets by two fishermen, Messrs R. and A. Isaksson). It can be seen that *Bosmina coregoni* dominates in June—July, *Daphnia cristata* somewhat later (July—September). *Bythotrephes cederstroemi* occurs as food only in July—August. The frequency of the large copepods (*Eurytemora* and *Heterocope*) increased towards the autumn.

According to Appelberg (1977) the cisco fed in June 1975 mainly on *Bosmina*, *Cyclopidae*, *Holopedium*, *Bythotrephes* and calanoid copepods, in that order.

Pelagic smelt

As smelt in the present samples display very different habits whether being pelagic or dwelling close to the bottom, I have found it practical to treat the material caught by trawl separately from that caught by sinking gill nets.

Smelt do not feed on *Cladocera* to the same extent as do cisco (Fig. 5), although even with this species the big *Bythotrephes cederstroemi* and *Leptodora kindti* are important food items. Of greater importance, however, were, in September 1972, the copepod *Heterocope appendiculata* and, in August, *Mysis relicta*. The latter species had not occurred at all as food of cisco in the pelagic samples in the autumn.

In Appelberg's (1977) samples from June 1975, *Mysis*, *Bosmina*, *Cyclopidae* and calanoid copepods (especially *Heterocope*) were predominant.

Svärdson (1958) has suggested that the smelt in Vänern should be ranked as two species: a small (10—15 cm), slow-growing species ("nors") and a larger (around 30 cm), fast-growing species ("slom"). It is of interest that large specimens in the present material had been feeding on fish. In contrast to the cisco, the smelt also feed heavily on amphipods (August 1973): *Gammaracanthus* and *Pallasea* as well as *Mysis relicta*.

To venture a rough generalization, the smelt can be said to give the impression of being a "miniature predator", judging both by its food habits and by its morphology (spool-shaped and with a rich set of sharp teeth).

In Fig. 8 an attempt has been made to illustrate a possible variation in the food habits of cisco and smelt depending both on the time of day and on the depth at which the fish were caught. Certain tendencies, albeit very vague ones, can be discerned.

Cladocera (*Bosmina coregoni*, *Limnosida frontosa*, *Daphnia cristata*) are mainly found as food of fish caught at the depth of 0—20 m. This is not, however, true of *Bythotrephes cederstroemi*, which is rather more frequent at greater depths. Smelt feeding on *Mysis relicta*

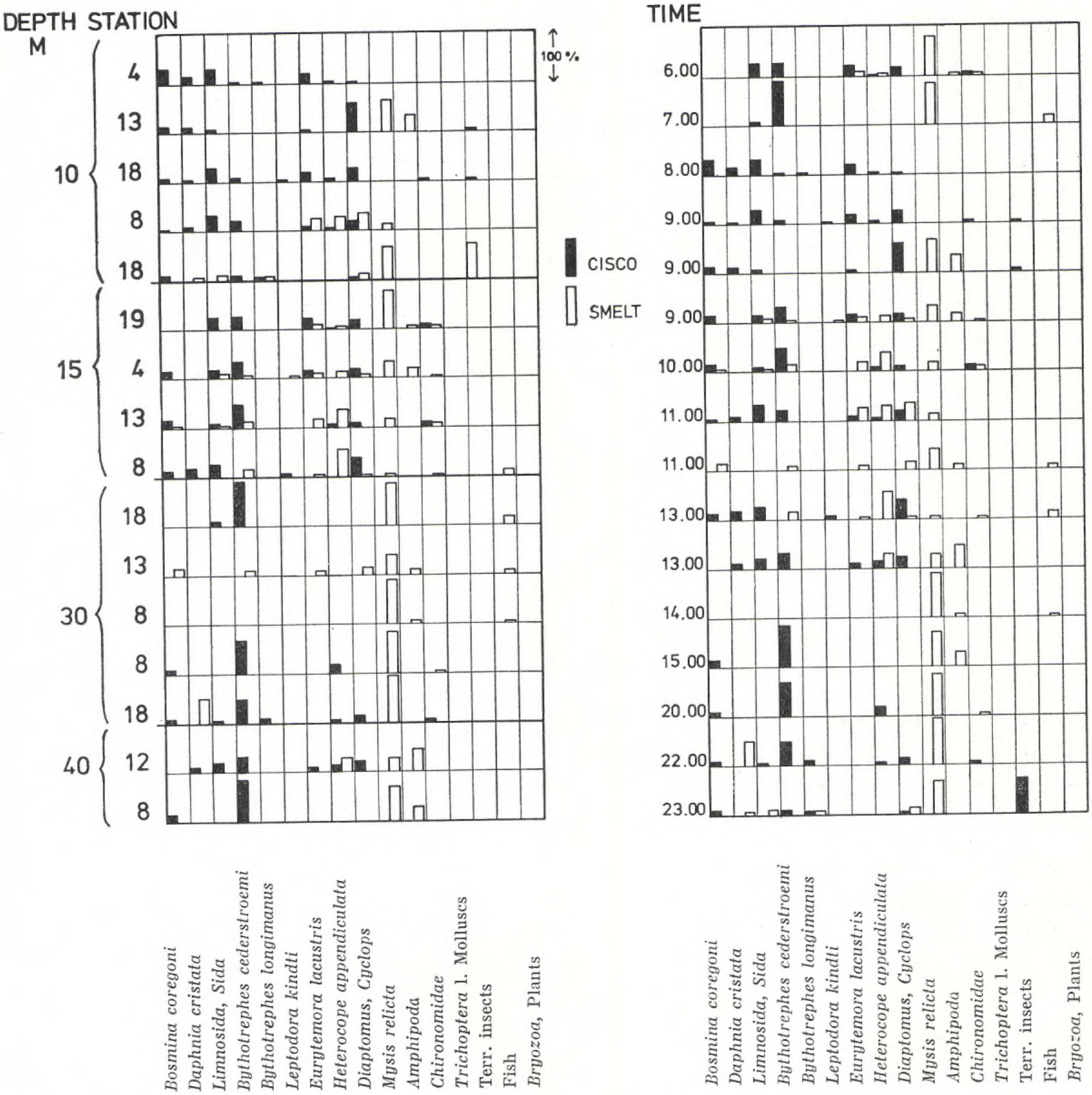

Fig. 8. The food habits of cisco and smelt caught at different depths (left) and times of the day (right) in September 1973.

are also somewhat more frequent at greater depths. The copepods (*Eurytemora*, *Heterocope appendiculata* and *Diaptomus gracilis*) occur as food of fish caught at 0—20 m as also do the small *Cladocera*.

In view, however, of the diel migrations of the fish and the rate of digestion at different temperatures and other parameters, no far-reaching conclusions can be drawn from this material. Nevertheless it supports the theory that there may be a state of competition between the two species, resulting in a segregation as regards both habitat and food selection.

The difference in numbers between the catches of the two species points to the possibility that,

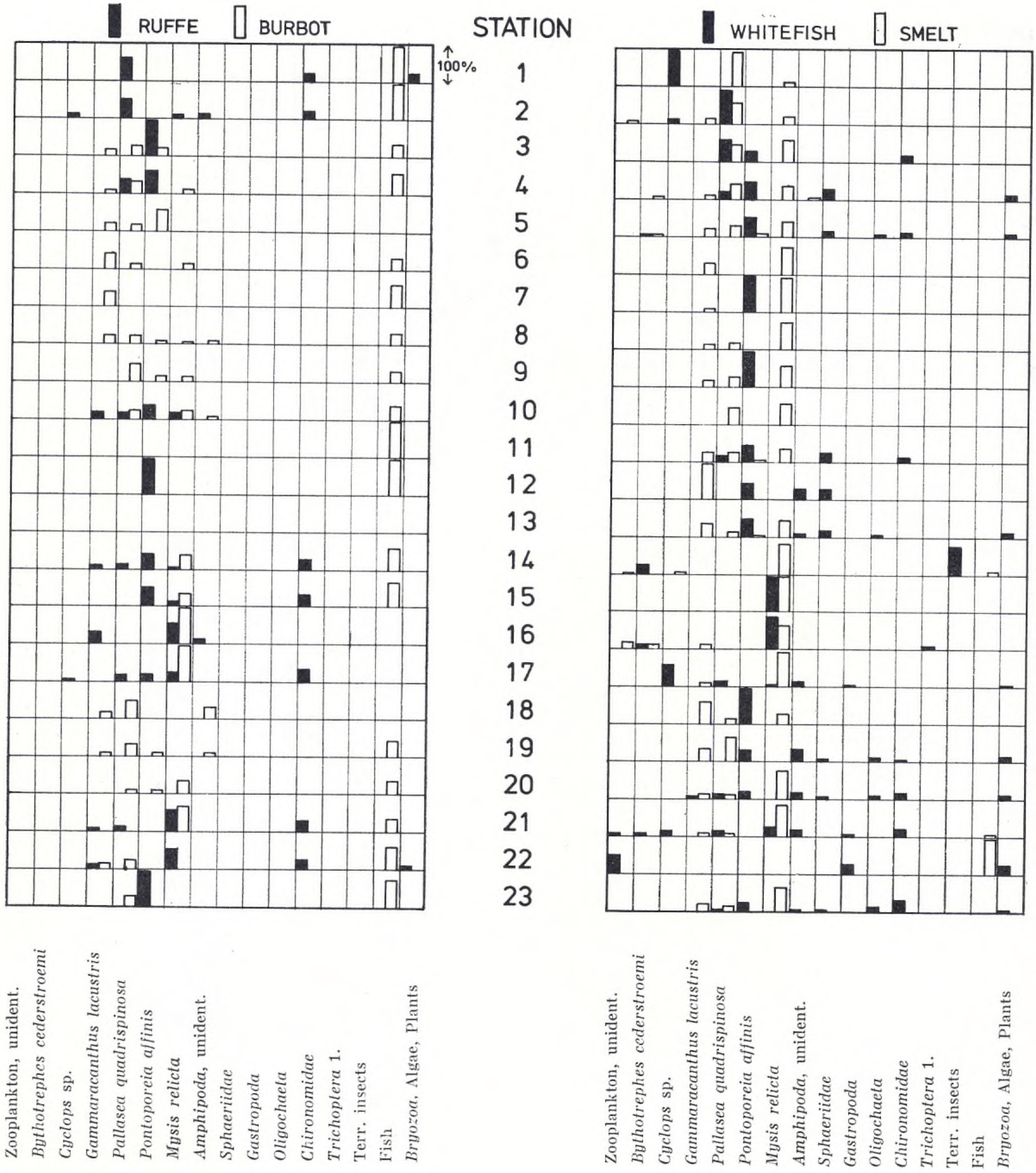

Fig. 9. The food of benthic fish, July—August 1973.

in Vänern, cisco is the dominant species, which theoretically should have the effect of forcing the smelt to segregate into a "predatory" niche. This agrees with the theories of "interactive segregation" and "interspecific population dominance" (NILSSON 1967, SVÄRDSON 1976).

Whitefish

Whitefish occur in Vänern as five species (SVÄRDSON and FREIDENFELT 1974, SVÄRDSON 1979), which can be distinguished by gill-raker counts, morphology, etc. They have been named in

Swedish "lövsik", "sandsik", "näbbsik", "gråsik" and "mårtensik". Their taxonomy and ecology was recently dealt with by SVÄRDSON (1979).

The whitefish caught by trawl in 1972 and 1973 consisted mainly of "gråsik" (B. ALMER, pers. comm.), which seems to be more pelagic than the other species. From Fig. 5 is clear that the food of whitefish in August 1972 consisted almost entirely of *Bythotrephes cederstroemi*, mixed with *Pontoporeia affinis* and *Trichoptera*.

In September benthic animals were more abundant: *Pontoporeia*, *Gammaracanthus*, *Pallasea*, chironomid larvae (*Monodiamesa*, *Heterotrissocladius*) and molluscs (*Pisidium*). But winged insects, which must have been caught at the surface, were also abundant.

Roach

The food of roach (Fig. 5) in August actually consisted entirely of *Bythotrephes cederstroemi*, mixed to some extent with terrestrial insects and plant fragments.

IV. THE BENTHIC FISH

Burbot (*Lota lota*), with a few exceptions, and ruffe (*Gymnocephalus cernua*) were not caught at all in the trawl fishery. They are entirely benthic species, which together with smelt and whitefish were caught at the greatest depths (down to 85 m).

The largest amounts of fish — as regards both numbers and standing crop — are found down to a depth of about 30 m.

Food habits

The food habits of the benthic fish can be seen from Fig. 9. The fish were all caught during the months of July and August 1973, and thus give no general picture of the food habits of the benthic fish during all seasons or years.

On the whole, however, the samples give a definite impression of homogeneity (as also did the pelagic fish), in spite of the fact that the different stations can reasonably be considered to cover most of the offshore ecosystems of the lake.

Whitefish

The whitefish caught on sinking gill-nets consisted mainly of "gråsik" *(cf.* SVÄRDSON and FREIDENFELT 1974), but some "näbbsik" also occurred. No difference between the food of the two species could be ascertained, as the material had to be brought together in one lump. It is obvious that, in contrast to the pelagic fish, the benthic species had mainly eaten benthic animals, especially *Pontoporeia affinis* and *Pallasea quadrispinosa*.

Even large bottom-living species of *Cyclops* occur, as well as *Sphaeriidae* and *Chironomidae*.

According to WIEDERHOLM (1978) the dominating benthic invertebrates in the offshore region are *Pontoporeia affinis*, *Oligochaeta*, *Pisidium* and *Chironomidae* (*Heterotrissocladius subpilosus*, *Micropsectra* spp. and *Paracladopelma obscura*).

Benthic smelt

The smelt had mainly eaten *Mysis relicta*, *Gammaracanthus lacustris* and *Pallasea quadrispinosa*, evenly over all stations. The low occurrence of planktonic *Crustacea* is obvious, but so also is the smelt's special ability to catch *Mysis*. *Gammaracanthus lacustris* and *Pallasea quadrispinosa* are in the main distributed evenly over all stations of the lake. The main difference between pelagic and benthic smelt is the almost complete absence of planktonic *Crustacea* in the latter. The characterization of smelt as being a "miniature predator" is confirmed. Maybe the ability of smelt to catch large relicts at great depths is what ultimately enables it to stand up to the competition from cisco.

Ruffe

Ruffe is a markedly benthic species. Owing to its great abundance, which is no doubt due to efficient feeding, it plays a prominent part in most southern Swedish lakes. In Vänern glacial relicts constituted the chief food of the ruffe, the most important species during the investigation period being *Pallasea quadrispinosa* and *Pontoporeia affinis*, as well as in the south-western parts of the lake, *Mysis relicta*.

Burbot

The burbot also mainly fed on the relicts *Gammaracanthus*, *Pallasea*, *Pontoporeia* and *Mysis relicta*. Of special significance, however, is the burbot's role as a fish-eater. At nearly all sampling stations fish (smelt and small cisco) were the most important food items.

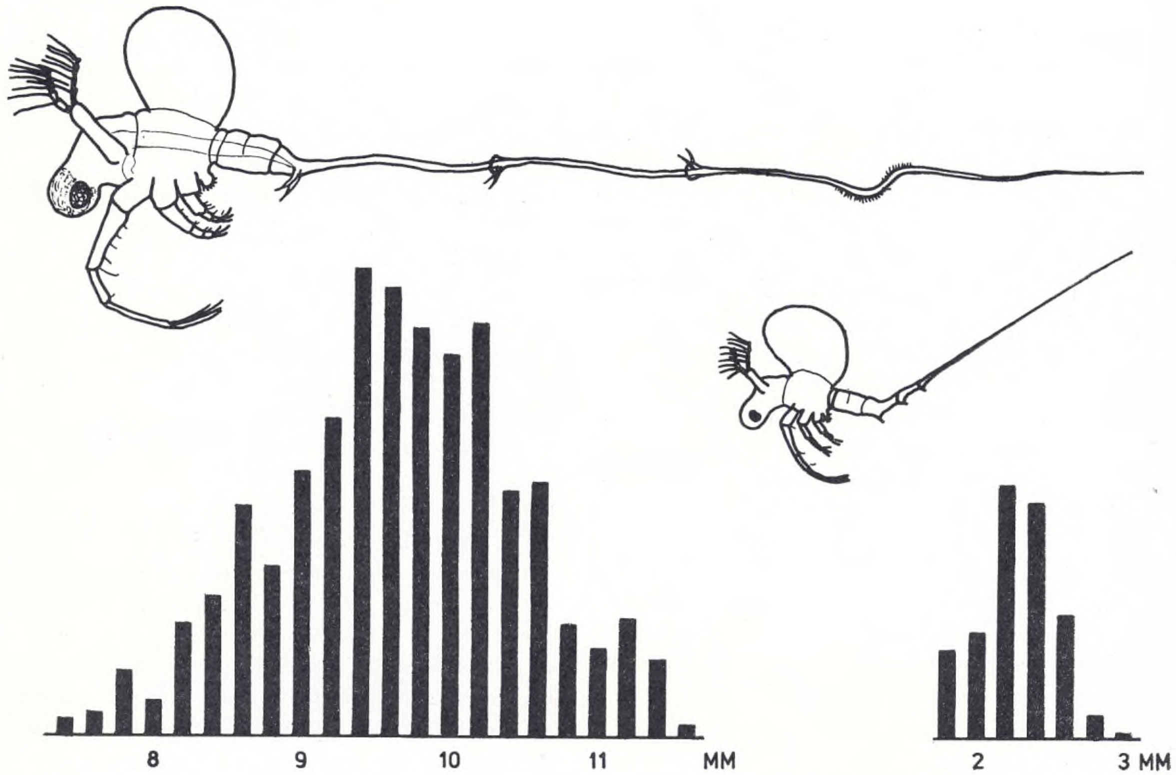

Fig. 10. The size distribution of mature *Bythotrephes cederstroemi* SCHOEDLER (left) and *B. longimanus* LEYDIG (right) found in fish stomachs from Lake Vänern, August—September 1972—73.

Sander

The (pike-perch) *Stizostedion lucioperca* is also mainly a fish-eater, sander with smelt mixed with small cisco as its main food. This was evident both for pelagic and for benthic specimens.

Bream

In Vänern, as in other lakes in Sweden, bream *Abramis brama* is typically a benthic species, although it has also been caught by trawl at most stations in Värmlandssjön. Through its mouth apparatus it can also reach prey as little accessible as oligochaetes.

V. THE SIGNIFICANCE OF *BYTHOTREPHES CEDERSTROEMI*

The very great importance as food of the cladoceran *Bythotrephes cederstroemi* was a surprise. The importance of this cladoceran could hardly be biased; it was found to be a major food item in the whole of Vänern for most pelagic species of fish during the autumn both of 1972 and of 1973, and APPELBERG (1977) reports *Bythotrephes* as food in June 1975.

Bythotrephes cederstroemi was first described by SCHOEDLER (1877), who obtained his samples from the Swede G. C. CEDERSTRÖM, who was at the time "instructor of fishery and fish culture" in the country. At about the same time W. LILLJEBORG in Uppsala (1861—1908) had started his great work on the *Cladocera* of Scandinavia (LILLJEBORG 1900). There he distinguished between two species of *Bythotrephes*, *viz. B. longimanus* LEYDIG and *B. cederstroemii* SCHOEDLER, with a number of varieties. The latter species is here called *B. cederstroemi* (it is named *cederströmii* by HERBST, 1962, and *cederströmi* by SCOURFIELD and HARDING 1966).

It is Lilljeborg's "variety" *cederstroemi s. str.* which plays such an important part as food in Vänern. It is much larger than *B. longimanus s. str.* (Fig. 10) and was noted by Lilljeborg in only seven lakes. Before the present investigation it was found in Vänern only by Pejler (1975).

There is little doubt that the two forms of *Bythotrephes* do in fact represent different species (Fig. 10). It is remarkable that though so important as a food it almost escaped sampling with plankton nets. Wesenberg-Lund (1937) compared polyphemids (including *Bythotrephes*) to dragonflies, and indeed it is easy to imagine that *Bythotrephes*, like dragonflies, hunt their prey by making sudden dashes. Their good vision (large eyes) is here of great importance. It may also protect them from such a big and "blind" predator as a plankton net.

The peculiar distribution of *Bythotrephes cederstroemi* is difficult to explain. Is it a glacial relict, or is it favoured by specific predatory habits of certain fish communities? For fishery management this question is of some importance in view of the value of the species as prey, and its very restricted distribution, which could be an argument for transplantations.

VI. SUMMARY AND CONCLUSIONS

This paper deals with the food habits of the fish community of the "offshore" region of Lake Vänern, that is to say the pelagic species, and the species that dwell close to the bottom outside the shallow bays. This means that several important species, for example pike and perch, have been left for further consideration. The present investigation is intended as a basic study, which should be easy to repeat in the future if changes should occur within the lake or in its fish community.

The cisco is the "dominant" fish species of the lake. This fits in with Svärdson's (1976) statement that "the dominance of some fish species seems correlated to the capacity to catch small-sized zooplankton, which has far-reaching consequences for the plankton fauna and hence primary production". Cisco is, like other pelagic species, migratory both horizontally and vertically, a fact which among other things is probably a reflection of the abundance of food. The currents referred to at the beginning of this paper, resulting as they do in an accumulation of nourishment at certain areas, should in that context play an important part, not only for the fish itself but for the fishery as well.

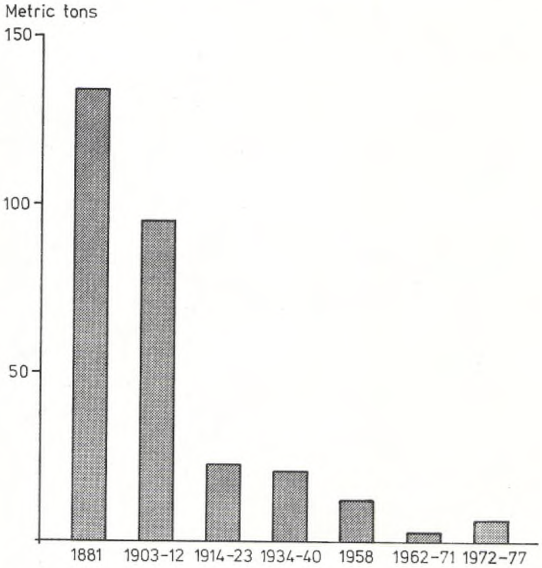

Fig. 11. The average catch of salmon and brown trout in Vänern 1881—1977 (from Almer 1978).

The smelt appears to be the most important food for the piscivorous species sander, burbot and salmon. The average size of the adult smelt varies between 150 mm (pelagic fish) and 175 mm (benthic fish) (Fig. 4). This size seems to be optimal, especially for the salmon, as even relatively small specimens in the present material had fed on average-sized smelt (Fig. 6). In any case the importance of smelt as food of large piscivores seems extraordinarily great. Svärdson (1976) has stated that "if the average size of the smelt is significant for the survival of a valuable predator a long-term change of the size of the smelt would have grave consequences. As whitefish and cisco, probably because of phosphate fertilization, have increased their growth rate in Vänern, one could expect a similar trend as to smelt". The fact that, besides smelt, the salmon also feed on the, on average larger-sized cisco, indicates that the situation as regards salmon is not yet critical in that context.

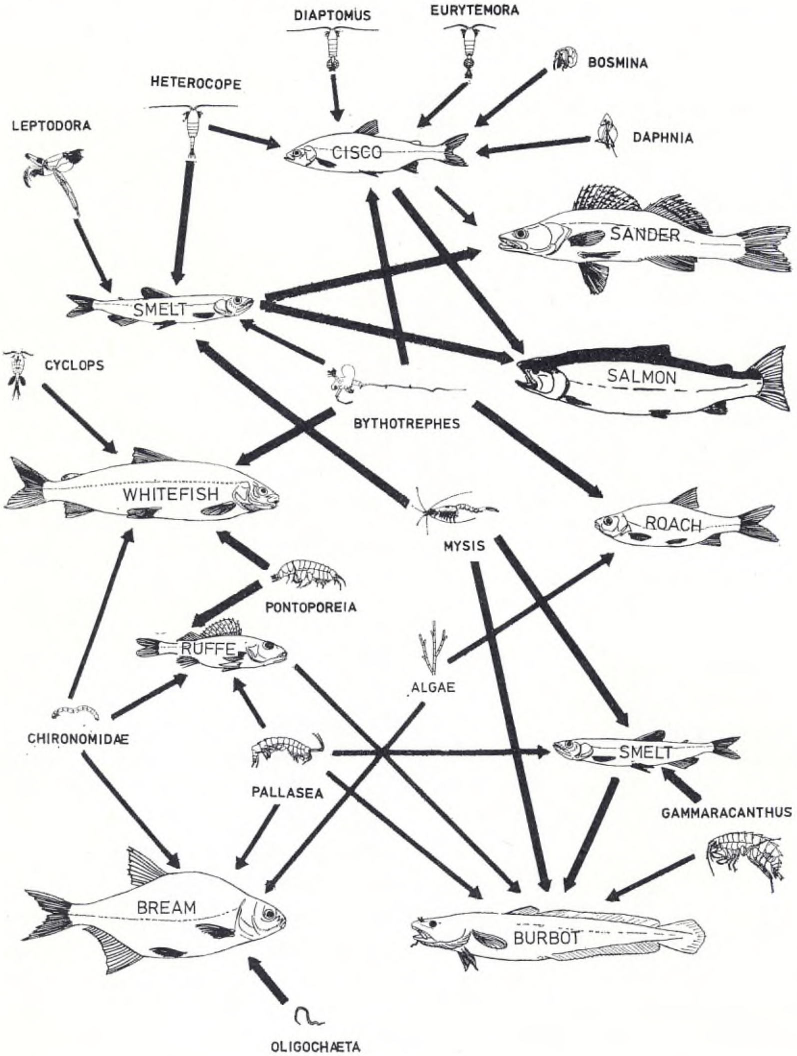

Fig. 12. Model of the food web in the offshore region of Lake Vänern (July—September 1972—73).

For non-piscivorous fish the large cladoceran *Bythotrephes cederstroemi* and the glacial relicts (especially *Mysis relicta*) were of fundamental importance during the years covered by the investigation. If smelt and these crustaceans are equally important in the long run the management of the fishery should be concentrated on them and on the valuable species of fish.

Of highest priority in this context is the salmon, especially the stock from River Gullspångsälven. The National Board of Fisheries, Sweden, has established that at least 80,000 reared smolt shall be released into the lake every year and the aim is to reach a catch of about 100 tons of salmon per year. In what degree this will influence the production of prey species (smelt and cisco) and possible competitors (sander, pike, perch and burbot) is a matter that remains to be studied. Fig. 11 shows the commercial catch of salmon and trout during the years 1881—1972. The decline is mainly the result of hydro-electric development.

Fig. 12 gives a rough idea of the complicated relationships between the different fish species of the offshore region of Lake Vänern and their prey. It can readily be imagined that any change in the food web would affect all species of fish in the lake.

VII ACKNOWLEDGMENTS

I thank Mr Brodde Almer for his enthusiastic planning of this expedition, as well as the fishermen of Lake Vänern for their cooperation. The stomach analyses were carefully made by Mrss Margit Andersson, Gunnel Hasselrot and Gun Svensson, the drawings by Mrs Monica Bergman. Mrs Bibi Ericsson brought order to the manuscript.

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Production and Food Consumption of Perch, *Perca fluviatilis* L., in Two Swedish Forest Lakes

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CONTENTS

I. INTRODUCTION

Together with pike (*Esox lucius* L.) and burbot (*Lota lota* L.), perch (*Perca fluviatilis* L.) is the most common freshwater fish in Sweden, being found in all parts of the country with the exception of the most northerly mountain regions (ANDERSSON 1964).

In a fishing inventory of Värmland County, undertaken just before the turn of the century, it was found that 1,919 of 2,030 waters contained perch (CEDERSTRÖM 1895). It is thus hardly surprising that the perch should have been the object of numerous and comprehensive investigations over a long period.

The studies carried out in Sweden have concentrated primarily upon the growth and food of the perch, special attention has been devoted to the reasons underlying the poor growth exhibited by perch in numerous waters, particularly in small and mostly humic forest or bog lakes (ALM 1922, 1939, 1946, 1952 and 1959). In an international perspective, the most comprehensive studies of perch have been carried out by LE CREN (1951, 1955, 1958, 1965 and 1977).

The purpose of the present investigation was to study the growth, population density, production and food consumption of perch in two small forest lakes with relatively simple ecosystems.

Since the early 1950s, numerous studies of fish production in fresh waters have been carried out in various countries (ALLEN 1951, GERKING 1962, MANN 1965 etc.).

In order to comprehend the role played by fish in the ecosystem, it is necessary to calculate in some way the consumption of various food organisms. Such studies have been carried out in several countries, particularly since WINBERG's major work of 1956 (MANN 1965, BACKIEL 1971). Owing to a lack of population and production studies, it has not previously been possible to study quantitatively the role played by fish in ecosystems in Sweden. The relatively simple com-

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Table 1. *The morphometric and more important physical-chemical parameters in Lakes Vitalampa and Botjärn 1968—72.*

	Vitalampa	Botjärn
Area (ha)	2.9	9.7
Maximum depth (m)	10.1	14.4
Mean depth (m)	2.8	3.3
pH	4.9—5.4	5.5—5.7
Colour (mg Pt/l)	60—85	70—120
Conductivity (mS/m (20°))	1.7—1.9	2.3—2.7
Total N (mg/l)	0.35—0.50	0.30—0.50
Total P (mg/l)	0.013—0.020	0.010—0.017

position of the ecosystem in lakes of the type at issue here (with only a few species of food organisms and frequently only one species of fish) makes such lakes particularly appropriate for these studies.

The present investigation was performed as part of the Kloten Project (Ramberg *et al.* 1973), the general purpose of which is the study of "the effects of forest fertilization and clear-cutting on ground and water". The same material has been interpreted in greater detail in an earlier publication (Nyberg 1976).

II. AREA OF INVESTIGATION

The two lakes investigated, Vitalampa and Botjärn, are located some 200 km north-west of Stockholm and drain into the Arboga River. The area is located above the highest post-glacial coastline and lies at c. 280 m above sea level. The bedrock consists primarily of younger granites, and the ground of moraine (Högbom and Lundqvist 1930).

The climate of the area, which lies within the northern conifer region is relatively severe, with permanent snow cover for 140 days of the year (averaged over 1901—30; Atlas över Sverige 1953).

Lake Vitalampa is a seepage lake and drains into Lake Botjärn. Table 1 illustrates the morphometric and more important physical-chemical parameters of the lakes. The latter parameters are average values for the whole water body, based on the lowest and highest values measured during the period March 1968—June 1972 (Ramberg *et al.* 1973).

Among phytoplankton, the dominating primary producers are (in Lake Vitalampa) *Chrysophyceae* and *Chlorococcales* and (in Lake Botjärn, which is more complicated than Lake Vitalampa) usually *Chrysophyceae* and *Dinophyceae* (Ramberg 1976). Among the higher plants, *Nuphar luteum* and (in Lake Botjärn) *Nymphaea alba* are the most important. Underwater vegetation in both lakes consists primarily of *Isoëtes echinospora*, *I. lacustris* and *Sphagnum subsecundum* (F. Eriksson, pers.comm.).

The greater part of the zooplankton population in Lakes Vitalampa and Botjärn, in terms of weight, consists of cladocerans, particularly *Holopedium gibberum*, *Bosmina coregoni* and *Daphnia cristata* (J.-Å. Johansson and H. Olofsson, pers.comm.).

In addition to *Chironomidae*, *Asellus aquaticus* and (in Lake Vitalampa) *Leptophlebia vespertina* are the dominating bottom animals within the vegetation area. On the bare bottom at greater depths *Chironomidae* dominate (Mossberg, pers. comm.).

The fish fauna in Lake Vitalampa consists only of perch. Lake Botjärn, however, does contain a small population of pike (*Esox lucius* L.) in addition to its numerous perch. In spite of intensive pike fishing (particularly during spawning), only 53 pike were caught during the period 1970—75, and in comparison with perch, the pike population may be considered negligible. It is probable that neither recreational nor household fishing has taken place in these lakes since the 1940s, so that the fish population may be said to be unaffected by fishing since then.

III. MATERIALS AND METHODS

Population estimates

Population estimates of the approximately one-month-old brood were carried out by means of a bag net 95 cm in diameter and with 0.8 mm mesh. The number of older fish was determined by the capture-recapture method. The fish were caught in fyke nets (10 mm mesh), marked by clipping part of a fin, and then released. One-year-old perch, however, were as a rule caught in a seine with 5 mm mesh.

During 1970—75, population estimates were carried out 19 times for Lake Vitalampa and 11 times for Lake Botjärn. In connection with fin-clipping, the total length of the fish was measured with an accuracy of 1 mm. The resulting material was divided into length classes at 5 mm intervals, and the perch population was thereafter divided into the following age groups: 0+, 1+, 2+ and >2+ in Lake Vitalampa; 0+, 1+ and >1+ in Lake Botjärn (1970—73); and 0+, 1+, 2+ and >2+ in Lake Botjärn (1974).

Recapture of fish marked during a season occurred primarily during spawning the following spring. The number of perch in the above-mentioned age groups was subsequently calculated according to the modified PETERSEN method,

$N = \frac{M(C+1)}{R+1}$, and the confidence limits with the aid of

$S_N = \frac{N^2(C-R)}{(C+1)(R+2)}$ (RICKER 1958, where M= number marked, C=number captured, R= number recaptured.

When determining the size of the spawning population, recapture was made during the experiment (SCHNABEL estimate). A division of the population was furthermore made into males and females, and the number of fish calculated as

$N = \frac{\Sigma C_t M_t}{\Sigma R + 1}$ (*op.cit.*), and the confidence limits as

$S_N = N \sqrt{\frac{N}{\Sigma C_t M_t}}$ (CHAPMAN 1954).

Two different methods for calculating the population have been applied. The reason for this is that calculations according to SCHNABEL can underestimate the magnitude of the population. Thus, it has been demonstrated that fish which have already once been caught in traps are more prone to be caught than other fish (BEUKEMA and DE VOS 1974). Furthermore, it has also been established that perch which have been captured and marked exhibit increased activity for some time after being released, and consequently are more likely to swim into the traps than are other fish (STOTT 1970). In addition, if the marked fish fail to mix fully with the unmarked ones, there is a danger of repeatedly capturing the same fraction of the population. If, on the other hand, the recapture occurs during spawning the following year, the marked fish will have been given a long period to calm down and mix with the unmarked ones; since this second fishing occurs under different conditions (spawning) from those obtaining during marking (food-seeking), the estimation of the size of the population should be more accurate. When determining the size of the spawning population, however, a SCHNABEL estimate seems to be the only possible method.

Growth

When determining growth in length for perch, age determinations and back-calculations have been made from the opercular bones (LE CREN 1947).

According to LE CREN (1958), perch require a water temperature of at least 13—14°C for growth, so that the actual growth seasons is regarded as extending from the middle of May until the middle of September (RAMBERG *et al.* 1973).

Production

Production has been calculated graphically according to the ALLEN method (ALLEN 1951), after first establishing the survival and growth curves (CHAPMAN 1968); the values used for the calculations have been taken from these. When calculating production in the age group 0+ in Lake Vitalampa, where in some cases numerical and weight values exist for a period of about 1 month after hatching and for the following spring, the mortality and growth curves have been assumed to exhibit exponential behaviour. According to CHAPMAN (*op.cit.*) this may in fact be assumed to apply to growth during at least the first year of the fish's life. For those years for which data are available only for one-year-olds, the survival curve has been assumed to possess the same directional coefficient as during the other years. In Lake Botjärn, however, data are (with few exceptions) lacking for the first year of the perch's life, and production there has been set approximately equal to the increase of biomass.

When calculating the ratio of production to biomass (P/B), the average annual biomass has been used.

Food

When ice covered the lakes, and occasionally during the rest of the year, collection of material for stomach analyses was effected with the help of gill nets. Upon capture, the perch were measured and weighed, after which their stomachs were preserved in 4 % formalin solution.

The greater part of the material was obtained, however, by capturing fish in fyke nets. After capture, the fish were measured, stomach-flushed and released. The stomach contents were preserved as described above.

The stomach contents of each individual perch were analysed under a stereomicroscope: the various prey were counted and determined as to species, genus or (in a few cases) family. The Chironomids found as perch prey were specified by PER MOSSBERG. This thorough analysis of the stomach contents was primarily designed to enable me to calculate as accurately as possible the wet weight of the food organisms and the stomach contents. The conversion was performed by multiplying the number of bottom animals found in the food by the average weight (formalin weight) of each relevant species in the lakes at that period of time (MOSSBERG, pers.comm.). The weight of the plankton crustaceans, however, was calculated from their volume, their specific weight being assumed to be 1 g/cm^3. A single annual value was used for each zooplankton species, however, this being the mean weight of the species in the lake (JOHANSSON and OLOFSSON, pers. comm.).

No attention was paid to the probably selective consumption of the largest animals in the prey population (GERKING 1962, GALBRAITH 1967), so that it is possible that the weight values used here are somewhat too low, both for zooplankton and for bottom animals. The amount of indigestible chitin varies from one animal group to another GENG 1925), so that in my opinion the method described above probably yields a value for the weight of the organisms comprising perch food that is more accurate than the value obtained via weight (GERKING 1962) or volume determinations (NILSSON 1955) of the organisms or organism remains in the stomach.

Metabolism

The annual energy consumption of the perch populations has been calculated according to WINBERG (1956): $Q = a \cdot W^k$, (Q_{Winberg}), where Q is the O_2-consumption in ml O_2/hour at 20°C, W is the weight of the fish and a and k are constants. With few exceptions, freshwater fish have the formula $Q = 0.336 \cdot W^{0.8}$ (*op.cit.*). MANN (1965), too, has shown that the formula is valid for perch, and it has therefore been used in the present work. The oxygen consumption at temperatures other than 20°C has been calculated according to KROGH (1916).

WINBERG's equation gives a measure of "routine metabolism", which he defines as the metabolism for a moderately active fish with no food in its stomach. In order to obtain conditions more closely resembling natural conditions, respiration tests were made with fish which had been fed. These experiments were carried out at various temperatures for fish in size groups 1+, 2+, and > 2+, in the following manner. The perch were caught in Lake Vitalampa and transferred to two temperature-controlled laboratory aquaria (500 l.) with a slow water circulation. During the first two weeks the fish were fed with worms (species of *Lumbricus*) and provided with ample supplies of food. For some 5—20 hours (depending upon the water temperature) before the experiment started, the perch were fed with a food amount which, according to the above-cited formula, was calculated to be equivalent to one day's supply in terms of energy requirements (maintenance level). The fish were then transferred to round-bottomed flasks (2—4 l.) within the aquaria and were allowed to acclimatize themselves under a slow water circulation for 2—3 hours, after which the circulation was cut off. The experiments were stopped before the O_2-saturation in the water in the flasks dropped below 75—80 %. The fish were then weighed. The oxygen consumption was determined according to the modified WINKLER method, and then converted to energy consumption under the assumption that 1 mg $O_2 = 3.42$ cal (WARREN 1971). The experiments lasted from 1 to 3 hours

Table 2. *Energy content of food organisms (cal/g wet weight).*

Organism	Energy content (cal/g · w.w.)	Reference
Zooplankton	550	Alimov *et al. 1972* Hillbricht-Ilkowska *et al.* 1972
Chironomidae (Diptera)	5424 cal/g · dw 87 % H_2O	Cummins and Wuycheck 1971 Landahl and Nagell 1975
Other Diptera	613	Cummins and Wuycheck 1971
Ephemeroptera	1124	— „ —
Odonata	1009	— „ —
Megaloptera	971	— „ —
Trichoptera	971	— „ —
Coleoptera[1]	759	— „ —
Corixa[1] (Heteroptera)	„	— „ —
Asellus aquaticus (Crustacea)	628	Prus 1972
Haemopis sanguisuga[2] (Hirudinea)	645	Cummins and Wuycheck 1971
Perch (*P. fluviatilis*)	1344	Jezierska 1974
„ gonads	1700	Backiel 1971

[1] average value for Insecta.
[2] „ „ „ Annelida.

and were conducted during daylight hours. Respiration experiments were carried out for a total of 176 perch, and at 5 different temperatures.

Consumption

The annual food consumption per perch population has been calculated according to Winberg's (1956) balanced equation: Energy of the ration = (1.25) · (Energy of metabolism (Q) + Energy of weight increase (ΔB)). When calculating according to Winberg, the energy content of fish tissue has been assumed to be 1 kcal/g (wet weight) (*op.cit.*).

When calculating the consumption of the various food organisms, the results from the present respiration experiments have been used: the energy consumption thus measured has been multiplied by 1.5 for the growth season and by 1.1 for the remainder of the year, in order to compensate for perch activity under natural conditions (for further details, see p. 151—152). The energy content for the various food organisms has been assumed as listed in Table 2.

The energy consumption and food consumption of the perch populations have been calculated for 17 periods during the year, and then combined to give the annual consumption. During May to September the length of the period was *c.* 14 days, and during the remainder of the year *c.* 1—1.5 months (Fig. 5). In the middle of each period, stomach analyses were performed upon perch from both lakes, in order to calculate the consumption of the various food organisms during the year. The water temperature has been calculated as the average temperature of measurements at 0.5 and 2.0 m depth, the limits of the layer in which perch are usually to be found.

For the results in Table 5, it was not found possible to calculate the number and production of the youngest fish (0+) in Lake Botjärn during 1974, owing to the insufficient amount of data. In this section, however, an approximation of the number of fish and the growth in this size class has been made, based on the average value for mortality and growth rates during 1970—73. In this manner, the total food consumption in Lake Botjärn could be calculated.

Furthermore, knowledge of the feeding habits of class 0+ is scanty for both lakes, consequently, using the data available, I have assumed that the fish in this class ate the same food as did the perch that were one year older.

Table 3. *Population numbers used in mortality rates and production calculations.*

Date	Vitalampa				Botjärn			
	0+	1+	2+	>2+	0+	1+	>1+	
May 12, 1970		960	270	1,540		3,700	14,200	
July 30, 1970	2,350	840	185	1,450				
September 10, 1970	2,100	805	150	1,400	10,100	1,600	13,840	
(May 12, 1971)	930	690	65	800	3,600	1,500	12,850	
May 12, 1971		930	690	800		3,600	14,300	
August 8, 1971	1,760	805	650	800				
September 10, 1971	1,350	785	640	790	7,600	2,500	14,200	
(May 12, 1972)	240	700	520	760	2,600	2,300	14,100	
May 12, 1972		240	700	1,280		2,600	16,400	
July 25, 1972	3,000	170	670	1,250				
September 10, 1972	2,500	165	660	1,230	20,100	2,000	15,400	
(May 12, 1973)	600	155	570	1,160	7,200	1,800	13,500	
May 12, 1973		600	155	1,730		7,200	16,500	
September 10, 1973	1,250	280	150	1,100	49,000	4,550	13,200	
(May 12, 1974)	410	235	140	1,000	16,900	3,400	7,700	
							2+	>2+
May 12, 1974		410	235	1,140		16,900	3,400	7,700
June 18, 1974		180	230	1,135				
August 13, 1974	8,500	40	230	1,120				
August 27, 1974						16,100	3,000	6,700
September 10, 1974	7,600	30	230	1,110		16,100	2,900	6,500
(May 12, 1975)	2,540	25	210	1,040		15,600	2,800	5,400

IV. RESULTS AND DISCUSSION

Population size

Population estimates were usually carried out during spawning, before the start of the growing season (May—June), July—August and in October. During 1970—75, a total of 6,980 fish were marked in Lake Vitalampa and 18,656 in Lake Botjärn. The precision of the estimates was as a rule quite good and 95 % confidence limits were always within the range 10—110 % of the mean. During spawning, however, population estimates of female perch were difficult to carry out. This was due to the fact that female perch participate in spawning for only a short period, during which the entire convoluted egg-strand is laid. They subsequently guard their roe (FABRICIUS 1956) and cease to participate in spawning, so that, once captured and marked, the females can rarely be recaptured. Accordingly, the size of the spawning population has been calculated on the basis of the number of spawning males and the sex ratio found in the lakes during times other than spawning.

Population numbers used in production calculations are given in Table 3. These values have been calculated graphically from survival curves (such as Fig. 1) constructed for each year class. During the period of study, the population density of perch older than 0+ was 470—950 perch/ha in Lake Vitalampa and 1,590—2,890 perch/ha in Lake Botjärn. ALM (1952) found slightly higher numbers in the same type of lakes.

Size distribution

Length measurements were made on a total of 8,570 perch (3,911 during spawning) in Lake Vitalampa and 12,657 (9,230 during spawning) in Lake Botjärn. The results are illustrated in Figs. 2 and 3. In both lakes the perch are relatively small. In this respect the populations can be regarded as typical of the majority of "dystrophic" forest lakes in Sweden (ALM 1946). In Lake Vitalampa the fish only rarely reach a length of 19—20 cm, and the majority of the fish are usually to be found in the 12—18 cm length class. The perch population in Lake Botjärn is composed of individuals even smaller

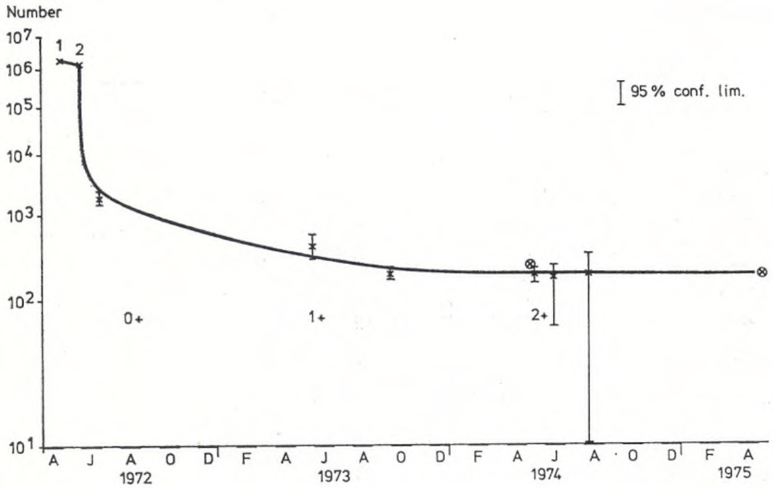

Fig. 1. The survival of perch hatched in spring 1972. (1 eggs; 2 *alevins* just after hatching; ⊗ population estimate during spawning.)

than those in Lake Vitalampa, the dominating length group being 9—15 cm. A comparison with earlier studies shows that the size distribution in Lakes Vitalampa and Botjärn is in quite good agreement with conditions in similar lakes (Alm 1921, 1946, Sumari 1971, Mossberg and Nyberg 1972).

The size distribution of perch during spawning is shown in Fig. 3. The majority of male perch begin to spawn at 2 years of age, having then a length of 9—12 cm in Lake Vitalampa and 8—10 cm in Lake Botjärn. The females, on the other hand, do not begin to spawn until one year later at the earliest, their lengths in the two lakes being then 12—14 cm and 10—12 cm, respectively. Alm (1952) found that males began to spawn at an age of 2—3 years and the females one year later. This is also in good agreement with Thorpe (1977 a).

Growth

The length growth of perch in Lakes Vitalampa and Botjärn is shown in Table 4 together with some values from other European waters. At one year of age the perch in the lakes studied has an average length of 5.4—6 cm. During their second growth season, the fish in Lake Vitalampa

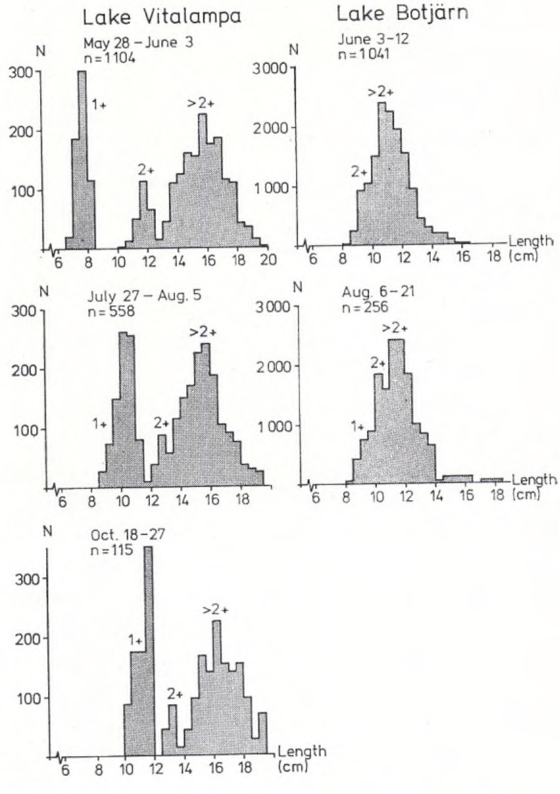

Fig. 2. The size distribution of the perch population in Lakes Vitalampa and Botjärn 1970.

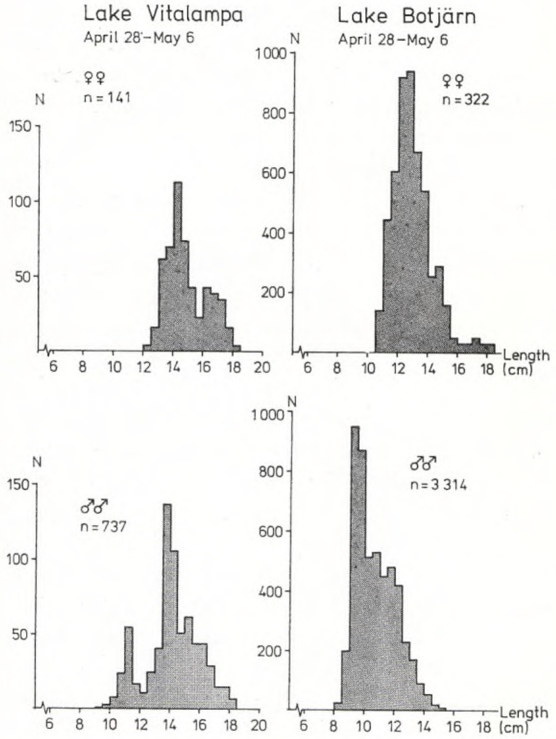

Fig. 3. The size distribution of the perch population during spawning in Lakes Vitalampa and Botjärn.

reach a length of 10.4 cm, while those in Lake Botjärn are smaller, being about 8.5 cm long. By the age of two years, the perch begin to grow more slowly in both lakes, and the annual growth rate thereafter decreases with increasing age. When 6 years old, the perch in Lake Vitalampa have reached a length of 16.5 cm and in Lake Botjärn 14.0 cm.

As can be seen from Table 4, the growth of perch in the two lakes studied is in quite good agreement with the growth of perch in other oligotrophic lakes in Scandinavia, but is far below what Tesch (1955) regarded as "poor growth". The table also shows that those waters where perch grow well even when older are as a rule large and rich in nutrients (*e.g.* Lake Hjälmaren, Lake Erken and the Baltic).

Reasons for the occurence of stunted perch populations

The reasons for the occurrence of stunted fish populations have been discussed over a long period. Alm (1946) quite early realized that the slow growth of perch was due to poor food supply, and above all to the fact that perch in small Swedish forest lakes only exceptionally take to feeding on fish. In larger lakes, by contrast, the food of grown perch usually consists of fish and often even small perch. Alm (1946) found that the difference between the two lake types was due partly to the fact that perch in forest lakes often ceased to grow at a very small size and partly to the lack of appropriate prey fish (above all smelt, *Osmerus eperlanus*).

A study of perch growth in Lake Vitalampa during the summer 1974 showed that young fish (1+) exhibited a quite good and constant growth throughout the season (Fig. 4), while fish one year older grew less well, particularly during July.

Table 4. *Perch growth in some European fresh waters.*

Lake	Country	Reference	Length (cm)						
			1	2	3	4	5	6	7
Vitalampa	Sweden		6.0	10.4	12.7	14.3	15.4	16.5	
Botjärn	”		5.4	8.5	10.5	11.9	13.0	14.0	15.5
Klotensjön	”	Alm 1921	2.8	5.3	7.7	10.2	12.4	14.3	16.6
St. Oivann	Norway	Deelder 1951	3.9	7.0	9.7	12.2	14.6	15.9	17.6
23 "ponds"	Finland	Sumari 1971	5.6	9.5	12.4	14.3	13.1	14.8	
Hjälmaren	Sweden	Alm 1946	3.9	7.9	11.6	15.6	19.5	22.6	25.8
Erken ♂♂	”	Agnedal 1968	6.6	10.2	12.9	14.3	15.5	17.0	18.8
” ♀♀	”	” ”	6.6	10.6	13.1	15.0	17.2	20.0	22.4
The Baltic ♀♀		Neuman 1976	6.7	10.3	14.3	17.1	19.2	20.8	22.0
"Poor growth"		Tesch 1955	8.0	12.2	14.8	18.9	21.8	25.2	31.4

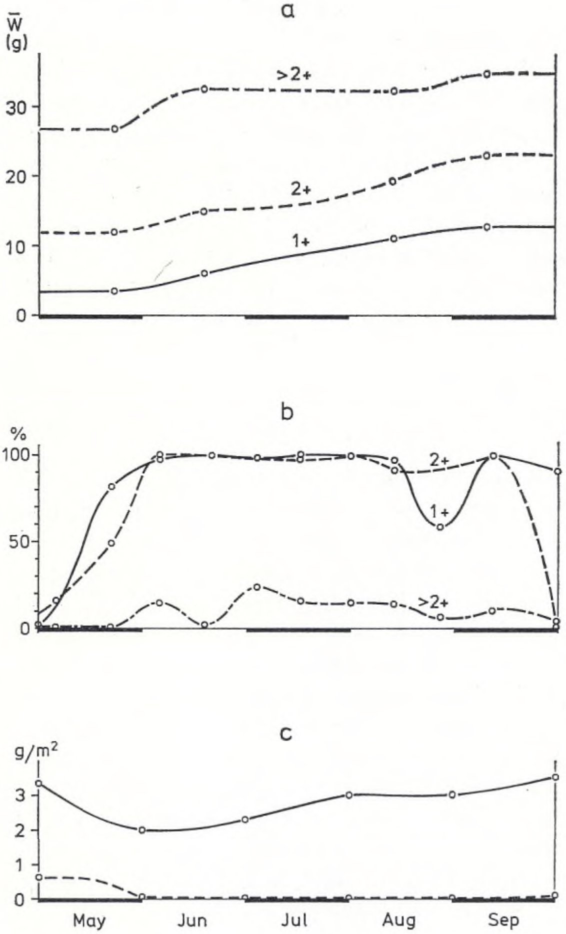

Fig. 4. a) The mean weight (g wet weight) of three size-classes of perch in Lake Vitalampa during May—September 1974. b) Relative weight of zooplankton (%) in the food of the same size-classes. c) Biomass of the bottom fauna (g wet weight/m²) during the same period (—— total bottom fauna, - - - *Asellus aquaticus* and *Leptophlebia vespertina*). (After Mossberg 1974.)

Growth among the older fish (> 2+) was reasonably satisfactory only during the early summer and the autumn, while such fish in fact diminished somewhat in weight during the summer. Backiel and Le Cren (1967) state that the fish growth in a population is, in normal situations, a function of fish density (see also Warren 1971), but that the type of lake studied by Alm is an exception to this rule.

When studying food habits of the perch in Lake Vitalampa, it was found that during the summer the younger fish (1+ and 2+) ate zooplankton almost exclusively (Fig. 4 b). During the growth season the stomach contents of even the older fish consisted to a relatively large extent of zooplankton (in terms of relative weight).

The reason why even the larger perch are forced to eat zooplankton during the summer is that the bottom fauna in forest lakes consists in large measure of insect larvae. The great majority of these hatch during the summer, so that the biomass of the bottom fauna is low during this period (Fig. 4 c). The only non-insect of importance here as perch food is *Asellus aquaticus*, but during the perch growth season this undergoes a generation shift, the old *Asellus* dying out and being replaced by young and small individuals (Mossberg, pers.comm.).

For fish, which are not adapted to feed on zooplankton, it becomes, with increasing fish size, more and more uneconomical, in terms of energy, to eat such animals (Kerr 1971). That is why large perch (> 2+), unlike the smaller ones, are in certain cases unable, by eating zooplankton, even to maintain their body weight during the summer, when the water temperature and thus also their metabolism are high. They therefore cease to grow quite early, and the transition to a diet of fish does not seem to take place.

Biomass and production

The average annual biomass was 1.8—2.5 g/m² in Lake Vitalampa and 1.8—4.0 g/m² in Lake Botjärn (Table 5). In Finnish ponds, without roach (*Rutilus rutilus*) and predatory fish, Sumari (1971) found biomasses around 2.0 g/m² (0.7—4.1 g/m²), when poisoning the ponds with rotenone. According to Carlander (1977) the biomass in percid lakes is 0.7—3.6 g/m² and in ponds and small lakes with only yellow perch (*Perca flavescens*) 3.9—21.5 g/m².

The total production of the perch population in Lake Vitalampa during 1970—74 was 0.7—1.2 g/m² · year (Table 5). The calculations for the total production in Lake Botjärn are rather more uncertain, as data are lacking for the brood's first year. When determining the increase in biomass in this age group, the mortality curves

Table 5. *Production (P), mean biomass ($\bar{B}$) (kg/lake and g/m^2 wet weight) and P/B ratios of the perch populations in the lakes studied.*

	Vitalampa				Botjärn			
Year	Age	P	$\bar{B}$	P/$\bar{B}$	Age	P	$\bar{B}$	P/$\bar{B}$
1970	0+	3.1	1.1	2.9	0+	(16)	11.3	(1.4)
,,	1+	9.1	6.5	1.4	1+	19.1	10.9	1.6
,,	2+	2.1	4.1	0.5	> 1+	92.5	246.7	0.4
,,	> 2+	14.9	60.3	0.2				
,,	Σ kg/lake	29.2	72.0			127.6	268.9	
,,	Σ g/m^2	1.0	2.5			1.3	2.8	
1971	0+	4.2	0.8	5.6	0+	(17)	12.3	(1.4)
,,	1+	8.6	5.2	1.7	1+	18.9	13.5	1.4
,,	2+	8.0	12.3	0.6	> 1+	112.6	184.0	0.6
,,	> 2+	13.6	43.0	0.3				
,,	Σ kg/lake	34.4	61.2			148.5	173.8	
,,	Σ g/m^2	1.2	2.1			1.5	1.8	
1972	0+	3.9	1.3	3.1	0+	(55)	39.6	(1.4)
,,	1+	2.0	1.3	1.5	1+	9.2	10.3	0.9
,,	2+	6.3	10.4	0.6	> 1+	71.6	287.2	0.3
,,	> 2+	8.7	40.8	0.2				
,,	Σ kg/lake	20.8	53.8			135.8	337.6	
,,	Σ g/m^2	0.7	1.9			1.4	3.5	
1973	0+	4.9	2.4	2.1	0+	(140)	99.3	(1.4)
,,	1+	4.8	3.0	1.6	1+	30.8	30.0	1.0
,,	2+	2.1	2.8	0.8	> 1+	87.6	256.1	0.3
,,	> 2+	15.1	43.3	0.3				
,,	Σ kg/lake	27.0	51.5			258.4	385.3	
,,	Σ g/m^2	0.9	1.8			2.7	4.0	
1974	0+	18.4	9.1	2.0	0+			
,,	1+	1.3	1.2	1.0	1+	62.5	82.2	0.8
,,	2+	2.6	4.2	0.6	2+	16.9	30.8	0.5
,,	> 2+	9.1	37.9	0.2	> 2+	50.6	138.7	0.4
,,	Σ kg/lake	31.4	52.4			139.0	251.8	
,,	Σ g/m^2	1.1	1.8			1.4	2.6	

have been assumed to follow the same pattern as in Lake Vitalampa, and the production is set approximately equal to the increase in biomass. If the mortality is very high at an early stage, this can serve as a relatively good approximation, but of course it invariably implies a value which is too low. For 1974, however, there exist no data whatsoever for the biomass in this age group. The total perch production in Lake Botjärn has been estimated to range from 1.3 to 2.7 g/m^2 · year, values which, considering the methods of calculation used, should be taken as minima. The highest annual value (2.7 g) is for 1973, a year marked by an unusually rich year class. The variations between the other years were less (1.3—1.5 g/m^2 · year), and the values were on the same level as for Lake Vitalampa.

Production of roe and milt constitutes a large proportion of the total production. During 1974 total production in age group > 2+ in Lake Vitalampa was 9.1 kg, of which some 4.5 kg (*c.* 50 %) may be estimated to consist of sexual organs. LE CREN (1962) found that, among sexually mature perch, production of roe and milt was about 42 % of the total production.

The P/$\bar{B}$ ratios listed in Table 5 show that the youngest fish are the most efficient: the ratio diminishes with increasing age. MATHEWS (1971) determined the P/$\bar{B}$ ratio for four species of fish in the Thames as: 0+ 2.6—3.6, 1+ 0.6—1.6, 2+ 0.8—1.0. This agrees quite well with the equivalent values from Lakes Vitalampa and Botjärn, with the exception of 0+ in Lake Botjärn, where (as noted above) the production value is too low.

There exist relatively few studies which include the entire fish production in lakes. This is due to difficulties in determining the number and growth of the young fish (0+ and 1+). As a rule, it is possible to determine the amount of roe deposited, but data are lacking for the following 2—3 years, until the fish reach the legal fishing limit or become sexually mature. In Lake Vitalampa, however, the data serving as a basis for production calculations are quite good.

Table 5 shows that the 0+ production during 1970—73 averaged 4 kg, out of a total average production of 27.8 kg, which is equivalent to approximately 14 % of the total fish production in the lake. In 1974 the latter was 31.4 kg, of which 18.4 kg came from the 0+ group, *i.e.* some 59 % of the total production.

Le Cren (1962) calculated the production of perch during their first two years in Lake Windermere (before 1941) based upon the amount of roe deposited and the number of fish after 2 years. There, he established that the production during this period was probably *c.* 58 % of the total production. Mathews (1971) studied the production of bleak (*Alburnus alburnus*), roach (*Rutilus rutilus*), gudgeon (*Gobio gobio*) and dace (*Leuciscus leuciscus*) in the Thames during their first year, and found that this group represented 39—73 % of the total production for all age groups. Despite of the uncertainty of Le Cren's (1962) values, it would seem clear that the production of one-summer-olds can constitute a very large proportion of the total production in a lake.

According to Chapman (1967) the fish production in the temperate areas in waters with one dominating fish species is normally 2—15 g/m². What, then, causes the relatively low production in Lakes Vitalampa and Botjärn?

In a fish population with a biomass which is disproportionately large in relation to the food supply, a very large part of the food consumed is used in standard metabolism and only a small part can be used for growth, so that production remains low (Warren 1971). The material from Lakes Vitalampa and Botjärn nevertheless does not indicate any correlation between the annual average biomass or the biomass at the beginning of the growing season, on the one hand, and production, on the other.

Johnson and Hasler (1954) studied the production of rainbow trout (*Salmo gairdneri*) in "dystrophic" lakes and found production values of 1.9—8.4 g/m² · year. They also found that the length of the growing season was of great importance for production. Gerking (1972) stresses that the length of the growing season is a crucial factor for production. The climate in the Kloten area is rather severe and the growth season for perch relatively short, circumstances which may be presumed to contribute to the low level of production.

Nevertheless, the most important contributory circumstance is probably the fact that these lakes are nutrient-poor (Ramberg *et al.* 1973, Ramberg 1976), and have a rather low production on other trophic levels (Eriksson *et al.* 1974), so that a high fish production is of course not to be expected. A calculation of the "trophic level production efficiency" (Odum 1971) for Lake Vitalampa yields an efficiency of 1.0—0.9 % during 1972—73. These values are rather low, according to Odum (10—20 %); this is probably attributable to the fact that 86—91% of the production in the lake on the lower production level consists of zooplankton (Eriksson *et al.* 1974), which cannot be fully utilized as food, especially for older perch.

Metabolism

The energy conversion and food consumption of fish may be given as

$C = F + U + \Delta B + R$, where

C = energy value of food consumed

F = energy value of faeces

U = energy value of materials excreted in the urine or through the gills or skin

ΔB = total change in energy value of materials of body (growth)

R = total energy of metabolism; this can be subdivided as follows: $R = R_s + R_d + R_a$, where

R_s = energy equivalent to that released in the course of metabolism of unfed and resting fish (standard metabolism)

R_d = additional energy released in the course of digestion, assimilation and storage of materials consumed (including specific dynamic action, SDA)

R_a = additional energy released in the course of swimming and other activity

(after Davis and Warren 1968).

The standard metabolism (R_s) should, according to numerous researchers (Brett 1964, Beamish and Dickie 1967, Warren 1971), be determined after a series of experiments with unfed fish having differing swimming activities. R_s is then obtained by extrapolating the activity to 0. According to the researchers in question, Winberg's "routine metabolism" is not sufficiently defined with respect to the nutritional status and activity of the fish, and is thus not applicable. Beamish (1964) found that R_s was *c.* 70 % of the routine metabolism calculated according to Winberg.

Respiration experiments

It has not been possible in the present work to study the importance that activity has for the metabolism. Impressions gathered during the experiments lead me, however, to regard the perch activity during the respiration experiments as reasonably equivalent to their activity in the lakes when resting (observations in connection with skin-diving).

According to the above-mentioned formula, fish metabolism increases after food intake (R_d). The purpose of the respiration experiments was primarily to obtain a measure of the sum of "R_s" (which in fact is not R_s according to the definition given above) and R_d. The increase in the metabolism depends, *inter alia*, upon the amount of food taken in and the activity of the fish in question (Warren 1971). Warren and Davis (1967) regard R_d as responsible for 8—38 % of the total metabolism. According to Beamish (1974), this amount is 14 %, according to Kerr (1971) about 30 % and according to Muir and Niimi (1972) 16—19 %.

Owing to the variation of R_d with the amount of food taken in, the perch were fed (some time before the start of the respiration experiments) with a food amount calculated so as to be approximately the same as the maintenance level. This food amount was chosen in the light of knowledge of the slight growth exhibited by fish in Lakes Vitalampa and Botjärn.

Except for experiments performed at very low water temperatures, the present respiration experiments with fed fish resulted in a higher O_2-consumption than that calculated according to Winberg (1956). Assuming that Winberg's equation gives the metabolism for moderately active unfed fish, the difference between the values given here and those given by Winberg may, if the activity of the fish is the same, be assumed to be due to the increased metabolism resulting from food ingestion. For the temperature range 14—17°C (where the perch growth occurs in these lakes), this difference comprises 10—20 % of the total metabolism, a value which agrees well with previously reported data in the literature concerning the size of R_d.

Energy requirements under "natural conditions"

The greatest difficulty in transferring the respiration results to natural conditions would seem to be the estimation of fish activity during the experiment and, above all, in natural conditions. The role played by activity in metabolism has been studied by, above all, Brett (1964, 1965), who found that fish in motion have a notably higher metabolism than when resting.

In Sweden the relative diel (*i.e.* 24-hours') activity of fish has been studied above all at the Messaure Biological Station in the northern part of the country (66°42'N, 20°25'E). Judging from Müller's results (1969, 1970 a, b), fish at this latitude are active for about 1/4—1/2 of the 24 hours. Eriksson (1975), who studied perch diel activity throughout the year at the station in question, found that, roughly speaking, they are active half of the 24 hours during May—September and about one third of the time during the winter. Andersson *et al.* (1972), who studied the diel winter activity of perch in Lake Erken, east of Uppsala (59°25'N, 18°15'E), arrived at similar results for that period.

There are, unfortunately, relatively few investigations concerning the degree of activity (swimming speed) of freshwater fish. Hergenrader and Hasler (1967) studied the swimming speed of yellow perch (*Perca flavescens*) in Lake Mendota, using a sonar; they found that the speed depended upon the water temperature (season), but that it was higher for fish in schools than for single fish. Their studies covered the time from immediately before sunrise until shortly after sunset. During that part of the day swimming speed averaged 12

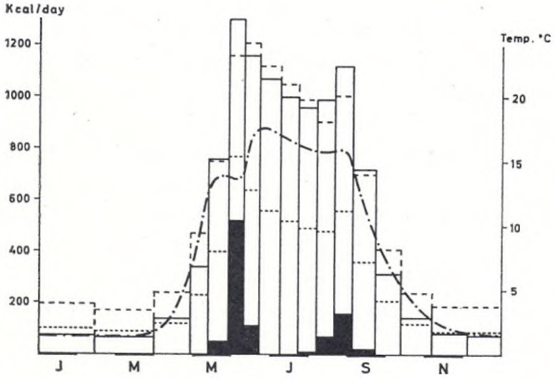

Fig. 5. Energy consumption (Kcal/class · 24h) in size-$>2+$ and water temperature (—·—) in Lake Vitalampa 1974. (☐ calculated consumption, ... Winberg I, - - - - - Winberg II, ■ growth.)

cm/sec at temperatures of 0—5°C, 17 cm/sec at 10—15°, and 20 cm/sec at 15—20°.

Taking the above data from the literature into consideration, I have assumed that during the growth season, perch in lakes Vitalampa and Botjärn are active during half of the 24 hours, and that during this time they swim at an average speed of 1 fish-length/sec. For the remainder of the year, they are assumed to be active during one third of the 24 hours, swimming at a speed of 0.5 fish-length/sec. According to Brett (1965), an activity of 0.5 fish-length/sec implies a metabolism increase of 1.3 times the standard metabolism, and an activity of 1 fish-length/sec an increase of approximately 2.0 times. The metabolism recorded during the respiration experiments has therefore been multiplied by 1.5 for the growth season and by 1.1 for the remainder of the year, in order to obtain the approximate energy consumption under natural circumstances.

Winberg (1956) states that his calculated routine metabolism should be multiplied by 2 in order to obtain a correct measure of the metabolism under natural conditions. According to Mann (1967) fish metabolism in natural conditions is 1.5—2.5 times Q_{Winberg}; if the routine-metabolism value is doubled, he states, we come within ±25 % of its true value in nature. Solomon and Brafield (1972) state that for low food consumption (up to the maintenance level, Winberg's routine metabolism seems to be correct, and that at higher consumption levels Q_{Winberg} should be multiplied by 1.5.

The results of the various methods of calculation are illustrated by the energy consumption/24 hours for the size class $>2+$ in Lake Vitalampa (Fig. 5). "Winberg I" is calculated as $Q_{\text{Winberg}}+\Delta B$ and "Winberg II" as $2 \cdot Q_{\text{Winberg}}+\Delta B$. It is obvious that the energy consumption calculated via respiration experiments is somewhat less than Winberg I for low water temperatures (January—March and November—December). For the temperature range 2—10° the consumption lies between Winberg I and II, and during the growth season it coincides quite well with Winberg II.

Food consumption

Winberg's (1956) balanced equation $C=1.25(R+\Delta B)$ presupposes that 80 % of the food consumed is used for metabolism and growth. Although this figure can vary, depending upon the qualitative and quantitative composition of the food and the metabolic status of the fish (Davis and Warren 1968), it would nevertheless seem to be a quite realistic average value. Using stomach analyses, the fresh weight and energy content of the food organisms and the values of energy consumption from the respiration experiments and the above-mentioned compensation for perch activity under natural conditions, the food consumption has been calculated according to that equation.

Values of food consumption of fishes given in the literature vary a great deal, partly depending on the methods used. As in the present paper, in most earlier works food consumption has been calculated from laboratory experiments. Thorpe (1977 b) criticizes such methods and considers that "estimates of daily ration which do not take into accout periodicity of feeding or field rates of evacuation must be misleading".

Daily ration

Fig. 6 illustrates the daily consumption of food of two different size classes of perch in Lake Vitalampa during 1974. In age group 1+ (size: 5—12 cm) food consumption was highest in June—July and the peak value was 9% wet weight of the body weight. The older perch

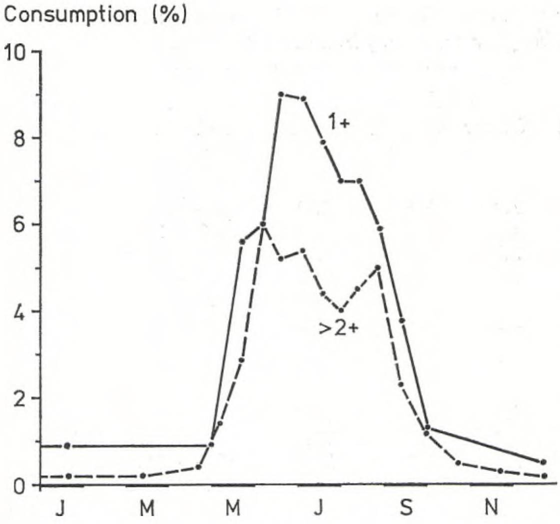

Fig. 6. Daily consumption of food by perch in Lake Vitalampa 1974 (wet weight in per cent of body weight).

(size: 14—19 cm) had a maximum consumption in May—June (6 %) and a tendency to a second peak in late August (5 %). According to THORPE (1977 b) perch of sizes 20—34 cm in Loch Leven in 1971 had a maximum daily consumption of 6.5 % in June and July, the value decreasing to 3.2 % in September. In 1972 the consumption was less. SCHNEIDER (1973) found that in 15.6—25.0°C the daily maintenance rations ranged between 2.0—5.0 % body weight depending on diet and that during excess feeding the values were 6.2—7.6 %. WURTSBAUGH and DAVIS (1977 a, b) found that juvenile rainbow trout (2.3—10.3 g) ate 2.0—7.0 % of the body weight/day and that at 16°C and near maintenance level the consumption was 4.1—5.2 % of the body weight, when the trout were fed with pellets.

In Lake Vitalampa the temperature rarely rises above 18°C and at least during summer the food for older perch apparently can be in short supply. The calculated food consumption may seem somewhat high, but as perch in Lake Vitalampa are much smaller than in THORPE's (1977 b) experiment, the daily consumption, expressed as % wet weight of body weight, should be higher than his values. THORPE (*op.cit.*) also considers that FORTHIN and MAGNIN's (1972) rations of 3.5 % and 3.6 % for perch > 15.6 cm and < 13.5 cm respectively cannot even meet the maintenance requirements of the fish.

Yearly consumption

Table 6 shows that during 1974 the perch population in Lake Botjärn consumed nearly 320 kg food/ha, and the population in Lake Vitalampa 136 kg/ha. The difference in consumption between these lakes is connected with the fact that the fish biomass/ha is greater in Lake Botjärn than in Lake Vitalampa, as well as with the fact that the average weight/fish is lower in the former lake.

Some 75 % of the ingested food is consumed during the growth season. A calculated growth season of about 4 months implies that 59 and 25 kg food/ha, respectively, is consumed each month. GERKING (1962) calculated the same consumption for bluegill sunfish (*Lepomis macrochirus*) in Wyland Lake at 87 kg/ha·month. MANN (1965) calculated the annual food consumption in the Thames as 7,050 kg/ha (705 kcal/m^2). That river, however, seems to be exceptionally productive, so that this particular comparison would seem to be less relevant.

A detailed study of the food consumed (Table 6) demonstrates that the cladocerans are the most important in both lakes. They are followed by *Asellus aquaticus* in Lake Botjärn, while in Lake Vitalampa chironomids rank second in order of importance. The production of food organisms in Lake Vitalampa shown in the table is from 1972 and 1973 (ERIKSSON *et al.* 1974), but presumably does not notably differ from that of 1974. Equivalent data from Lake Botjärn are unfortunately as yet unavailable.

The comparison between the calculated amount of consumed food and the production of the equivalent form of food seems to indicate that certain organism groups (*Ephemeroptera*, *Trichoptera*, and *Chironomidae*) are consumed in amounts exceeding those actually produced in the lake. This, of course, is impossible. The error presumably lies in an overcalculation of consumption or too low a measurement of the production of these animals.

Methodic "leaks" during sample-collecting, sieving and selection collectively result in too low a number of individuals being registered for the

Table 6. *Food consumption in Lakes Botjärn and Vitalampa (1974) in kg/ha (fresh weight), and production of food organisms (kg/ha year 1972—73) in Lake Vitalampa.*

Food type	Botjärn			Vitalampa			
	Winter	Growth season	Annual total	Winter	Growth season	Annual total	Food prod./ year
Cladocera	29.3	83.8	113.1	17.3	31.8	49.1	550 —850
Copepoda	4.5	20.1	24.6	1.0	3.4	4.4	20.2— 27.2
Asellus aq.	29.4	62.3	91.7	2.7	6.9	9.6	45.7— 33.9
Ephemeroptera	3.4	2.3	5.7	9.5	5.7	15.2	4.3— 4.4
Odonata	2.7	5.5	8.2	2.3	3.0	5.3	5.0— 3.9
Coleoptera				0.9	4.3	5.2	?
Megaloptera	2.7	1.3	4.0				
Trichoptera	2.3	20.8	23.1	0.8	9.9	10.7	9.1— 6.4
Chironomidae							
larvae	2.9	8.4	11.3	1.2	17.5	18.7	
pupae	0.3	14.5	14.8	1.2	8.9	10.1	
Σ Chironomidae	3.2	22.9	26.1	2.3	26.4	28.7	22.7— 18.8
Other bottom f.	3.2	6.8	10.0	0.7	2.3	3.0	12.7— 14.6
Fish		12.1	12.1				
Surface food					4.7	4.7	
Σ kg/ha	80.7	237.9	318.6	37.6	98.4	136.0	669.7—959.2
Fish prod. kg/ha		~14			11.0		

bottom animals in the lake. The production figures should therefore be regarded as minimum values, and the actual production as being in fact higher. During both early autumn and spring, *Leptophlebia vespertina* (*Ephemeroptera*) leads a pelagic life (KJELLBERG 1971, MOSSBERG, pers. comm.) and so cannot be quantitatively captured in bottom samples. A calculation of perch predation upon *Leptophlebia* during the months January—April shows that some $4.3 \cdot 10^6$ animals were consumed during this period. A calculation of mortality based upon bottom samples shows that some $3.8 \cdot 10^6$ animals died during the same period (MOSSBERG, pers.comm.). The perch seems to be the only predator of importance for *Leptophlebia* in this lake (*op.cit.*), so that the mortality may be regarded as being due to grazing by the perch population. The agreement between $4.3 \cdot 10^6$ (calculated predation) and $3.8 \cdot 10^6$ (found mortality) must be regarded as good, demonstrating that the consumption calculations during at least that period are reasonable.

V. SUMMARY

The purpose of the present investigation has been to study the production and food consumption of perch (*Perca fluviatilis* L.) in two small (2.9 and 9.7 ha respectively) forest lakes in Sweden. The lakes investigated are oligotrophic, with rather acid and brownish water. The fish population in Lake Vitalampa consists only of perch; that of Lake Botjärn also includes occasional pike (*Esox lucius* L.).

During the five years 1970—74, production was 0.7—1.2 g/m²·year and 1.3—2.7 g/m²·year (wet weight) for Lakes Vitalampa and Lake Botjärn, respectively. The highest production values were as a rule recorded for the years when the newly-hatched fry were particularly numerous. In Lake Vitalampa, the production of the older fish ($> 2+$) was calculated to consist to approximately 50 % of sexual products.

The annual food consumption was calculated with the aid of respiration experiments, under the assumption that 80 % of the food consumed can be assimilated. The food consumption of the perch population during 1974 was calculated to be 320 kg/ha in Lake Botjärn and 136 kg/ha in Lake Vitalampa (wet weight). Some 75 % of this amount was consumed during the growth season (approximately 4 months). The predation on bottom fauna in Lake Vitalampa was very intensive, whereas the perch were only to a very small

extent able to utilize the large zooplankton production in that lake.

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Accuracy and Robustness of Some Population Estimates Based On Multiple Marking. With Special Reference to Fresh-Water Fish

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CONTENTS

I. INTRODUCTION AND NOTATION

Multiple marking has become a widely used technique to estimate population size in many areas, especially in connection with fresh-water fish. Several estimates based on this technique have been developed and discussed mathematically, but for most of them only approximate formulas for bias and standard deviation have been found. Furthermore, the assumptions underlying them are generally not completely met with in practice, and little is known about the robustness of the estimates with regard to departures from these assumptions. In the present paper the accuracy and robustness of six of the most well-known population estimates based on multiple marking are analysed using Monte Carlo technique on a high speed computer.

In a multiple marking experiment several samples are taken from the population being studied. For each sample the marked individuals are noted; those not marked are marked, and then the whole sample is returned to the population.

The following notation will be used throughout:

N : The size of the population being studied when the first sample is taken.
M_i : The number of marked individuals in the population at the time the i-th sample is taken.
U_i : The number of unmarked individuals in the population at the time the i-th sample is taken.
n_i : The number of individuals taken in the i-th sample.
m_i : The number of marked individuals recovered in the i-th sample.
a_i : The proportion of unmarked individuals which leave the population between the i-th and the (i+1)-th sample.
b_i : The proportion of marked individuals which leave the population between the i-th and the (i+1)-th sample.
c_i : The proportion of individuals which enter the population between the i-th and the (i+1)-th sample.
s : The number of samples taken.

Estimates based on multiple marking were first developed by SCHNABEL (1938). As an estimate of N she proposed the unique root $\hat{N}_1$ of the equation

$$(1) \qquad \sum_{i=2}^{s} \frac{(n_i - m_i)\, M_i}{N - M_i} = \sum_{i=2}^{s} m_i$$

An approximate solution of this equation is

$$\hat{N}_2 = (\sum_{i=2}^{s} n_i\, M_i)/(\sum_{i=2}^{s} m_i)$$

Chapman (1952) proposed a modification of this estimate:

$$\hat{N}_3 = (\sum_{i=2}^{s} n_i M_i)/(\sum_{i=2}^{s} m_i + 1)$$

Schumacher and Eshmeyer (1943) proposed the estimate

$$\hat{N}_4 = (\sum_{i=2}^{s} n_i M_i^2)/(\sum_{i=2}^{s} m_i M_i)$$

Chapman (1952) proposed as an estimate of N the unique root $\hat{N}_5$ of the equation

$$\prod_{i=1}^{s} (1 - n_i/N) = 1 - r/N \quad (N \geqslant r) \tag{2}$$

where $r = \sum_{i=1}^{s} n_i - \sum_{i=2}^{s} m_i$. He also proposed the estimate

$$\hat{N}_6 = \frac{1}{s-1} \sum_{i=2}^{s} \frac{(n_i+1)\ (M_i+1)}{m_i+1} - 1$$

In Appendix 1 it is shown that equation (1) has a unique root, and that

$$a < \hat{N}_1 \leq a + M_s,$$

where $a = (\sum_{i=2}^{s} (n_i - m_i) M_i)/(\sum_{i=2}^{s} m_i)$. Thus the technique developed by Robson and Regier (1968) may be used to evaluate $\hat{N}$.

Seber (1973: 472—473) proved that equation (2) has a unique root greater than r, and in Appendix 2 it is shown that

$$\hat{N}_5 < (\sum_{i=2}^{s} n_i)^2/(2 \sum_{i=2}^{s} m_i)$$

Thus the technique of Robson and Regier may be used to evaluate $\hat{N}_5$.

Suppose that k independent multiple marking experiments have been simulated under identical conditions. A population estimate $\hat{N}$ will then generate k independent estimates $N_1, N_2 \cdots, N_k$ of the size of the simulated population. Expectation (μ) and standard deviation (σ) of $\hat{N}$ may then be estimated by the formulas

$$\hat{\mu} = \frac{1}{k} \sum_{i=1}^{k} N_i \tag{3}$$

$$\hat{\sigma} = \sqrt{\frac{1}{k-1} \sum_{i=1}^{k} (N_i - \hat{\mu})^2} \tag{4}$$

According to the central limit theorem $\hat{\mu}$ will be normally distributed when k is large, provided $\hat{N}$ has a finite variance. 95 % confidence limits for μ are then given by

$$\hat{\mu}_{1,\,2} = \hat{\mu} \pm 1.96\sigma/\sqrt{k} \tag{5}$$

As a measure of the robustness of $\hat{N}$ is used

$$R = \sqrt{\frac{1}{k} \sum_{i=1}^{k} (N - N_i)^2}$$

which may also be written

$$R = \sqrt{(N - \hat{\mu})^2 + (1 - \frac{1}{k})\ \hat{\sigma}^2} \tag{6}$$

II. SIMULATION PROCEDURES

A. If all the individuals in the population being studied are equally likely to be caught when a sample is taken, m_i will be hypergeometrically distributed with parameters $(U_i + M_i,\ M_i,\ n_i)$.

Generally some mortality, migration and recruitment will occur during the sampling period. $\{U_i\}$ and $\{M_i\}$ are then given by the equations

$$\left\{ \begin{array}{ll} M_{i+1} = (M_i + n_i - m_i)\ (1 - b_i) & (M_1 = 0) \\ U_{i+1} = (U_i - n_i + m_i)\ (1 - a_i) + (U_i + M_i)\ c_i & \\ (U_1 = N) & \end{array} \right. \tag{7}$$

Multiple marking experiments of this kind have been simulated on a high speed computer in the following way.

A procedure which generated hypergeometrically distributed numbers was written. Sample sizes $n_1 = 53$, $n_2 = 94$, $n_3 = 97$, $n_4 = 132$, $n_5 = 55$, $n_6 = 139$, $n_7 = 155$, $n_8 = 115$ obtained in a multiple marking experiment on minnows in a small Norwegian mountain lake were used as fixed parameters. For fixed values of N, s, $\{a_i\}$, $\{b_i\}$ and $\{c_i\}$ 2500 independent realisations of catch-data $\{m_i\}$ were generated by means of the hypergeometric procedure and the equations (7), and each time $\hat{N}_1, \hat{N}_2, \cdots, \hat{N}_6$ were calculated. Expectations and standard deviations of $\hat{N}_1, \hat{N}_2, \cdots, \hat{N}_6$ were then estimated by means of the formulas (3) and (4), and 95 % confidence limits for expectations were evaluated using formula (5).

In this way the bias and standard deviation of $\hat{N}_1, \hat{N}_2, \cdots, \hat{N}_6$ were examined for different values of N, s, $\{a_i\}$, $\{b_i\}$ and $\{c_i\}$, i.e. the accuracy of $\hat{N}_1, \hat{N}_2, \cdots, \hat{N}_6$ could be analysed, as well as the robustness against mortality, migration and recruitment.

B. If catchability is rather variable within a population, the marked individuals will generally be easier to catch than the unmarked. This trap response situation was simulated by replacing each M_i by k^*M_i ($k > 1$) before entering the hypergeometric procedure. The robustness of $\hat{N}_1$, $\hat{N}_2$, $\cdots$, $\hat{N}_6$ against "differentiated catchability" were then analysed quite similarly to in A; a_i, b_i and c_i in the equations (7) were equalled zero, and then bias and standard deviation of $\hat{N}_1$, $\hat{N}_2$, $\cdots$, $\hat{N}_6$ were examined for various values of N, s and k.

C. Another kind of trap response is "trap shyness", *i.e.* the marked individuals are generally less catchable than the unmarked. This situation was simulated quite similarly to in B, the only difference being that now $k < 1$.

III. RESULTS

Accuracy under ideal assumptions

The ideal multiple marking situation, *i.e.* when no mortality, recruitment, migration or trap response occur and each individual is equally likely to be caught when a sample is taken, was first simulated. Estimated expectation and standard deviation, confidence limits and robustness have been calculated by the formulas (3)—(6).

With 8 samples the simulations gave the following results:

Table 1. *Actual population size: 2000.*

Formula (a)	Estimated expectation (b)	Bias (c)	Estimated stand. dev. (d)	(μ_1, μ_2) (e)	Robustness (f)
$\hat{N}_1$	2010	10	149	(2004, 2016)	149
$\hat{N}_2$	2010	10	149	(2004, 2016)	149
$\hat{N}_3$	1996	—4	147	(1990, 2002)	147
$\hat{N}_4$	2010	10	154	(2004, 2016)	154
$\hat{N}_5$	2010	10	149	(2004, 2016)	149
$\hat{N}_6$	1979	—21	237	(1969, 1989)	238

Table 2. *Actual population size: 4000.*

a	b	c	d	e	f
$\hat{N}_1$	4037	37	455	(4019, 4055)	457
$\hat{N}_2$	4037	37	455	(4019, 4055)	457
$\hat{N}_3$	3981	—19	443	(3963, 3999)	443
$\hat{N}_4$	4041	41	475	(4022, 4060)	477
$\hat{N}_5$	4037	37	454	(4019, 4055)	456
$\hat{N}_6$	3827	—173	599	(3803, 3851)	624

Table 3. *Actual population size: 6000.*

a	b	c	d	e	f
$\hat{N}_1$	6109	109	860	(6075, 6143)	867
$\hat{N}_2$	6110	110	861	(6076, 6144)	868
$\hat{N}_3$	5983	—17	825	(5950, 6016)	825
$\hat{N}_4$	6118	118	909	(6082, 6154)	917
$\hat{N}_5$	6109	109	861	(6075, 6143)	868
$\hat{N}_6$	5558	—442	948	(5520, 5596)	1046

Table 4. *Actual population size: 10000.*

a	b	c	d	e	f
$\hat{N}_1$	10310	310	1968	(10231, 10389)	1992
$\hat{N}_2$	10311	311	1970	(10232, 10390)	1994
$\hat{N}_3$	9955	—45	1829	(9882, 10028)	1830
$\hat{N}_4$	10326	326	2059	(10244, 10408)	2085
$\hat{N}_5$	10310	310	1968	(10231, 10389)	1992
$\hat{N}_6$	8617	—1383	1680	(8550, 8674)	2176

Table 5. *With actual population size N= 2000 the simulations gave the following results:*
After 2 recatches:

a	b	c	d	e	f
$\hat{N}_1$	2214	214	879	(2179, 2249)	905
$\hat{N}_2$	2215	215	879	(2180, 2250)	905
$\hat{N}_3$	1957	—43	648	(1931, 1983)	649
$\hat{N}_4$	2252	252	1032	(2211, 2293)	1062
$\hat{N}_5$	2214	214	879	(2179, 2249)	905
$\hat{N}_6$	1917	—83	667	(1890, 1944)	672

Table 6. *After 4 recatches:*

a	b	c	d	e	f
$\hat{N}_1$	2049	49	344	(2035, 2063)	348
$\hat{N}_2$	2049	49	343	(2035, 2063)	347
$\hat{N}_3$	1989	—11	323	(1976, 2002)	323
$\hat{N}_4$	2060	60	370	(2045, 2075)	375
$\hat{N}_5$	2049	49	344	(2035, 2063)	348
$\hat{N}_6$	1957	—43	386	(1942, 1972)	388

Table 7. *After 6 recatches:*

a	b	c	d	e	f
$\hat{N}_1$	2015	15	177	(2008, 2022)	178
$\hat{N}_2$	2015	15	177	(2008, 2022)	178
$\hat{N}_3$	1996	—4	174	(1989, 2003)	174
$\hat{N}_4$	2017	17	185	(2010, 2024)	186
$\hat{N}_5$	2016	16	177	(2009, 2023)	178
$\hat{N}_6$	1977	—23	268	(1966, 1988)	269

Robustness against mortality

Situations with mortality were simulated with actual population size $N=4000$ and 8 samples. Results:

Table 8. *1 % of the population die between two subsequent samples:*

a	b	c	d	e	f
$\hat{N}_1$	3937	—63	435	(3920, 3954)	440
$\hat{N}_2$	3939	—61	436	(3922, 3956)	440
$\hat{N}_3$	3886	—114	424	(3869, 3903)	439
$\hat{N}_4$	3930	—70	453	(3912, 3948)	458
$\hat{N}_5$	3938	—62	435	(3921, 3955)	440
$\hat{N}_6$	3763	—237	587	(3740, 3786)	633

Table 9. *3 % of the population die between two subsequent samples:*

a	b	c	d	e	f
$\hat{N}_1$	3746	—254	400	(3730, 3762)	474
$\hat{N}_2$	3751	—249	401	(3735, 3767)	472
$\hat{N}_3$	3702	—298	391	(3687, 3717)	492
$\hat{N}_4$	3719	—281	412	(3703, 3735)	499
$\hat{N}_5$	3746	—254	400	(3730, 3762)	474
$\hat{N}_6$	3635	—365	568	(3613, 3657)	675

Table 10. *5 % of the population die between two subsequent samples:*

a	b	c	d	e	f
$\hat{N}_1$	3547	—453	364	(3533, 3561)	581
$\hat{N}_2$	3556	—444	365	(3542, 3570)	575
$\hat{N}_3$	3512	—488	357	(3498, 3526)	605
$\hat{N}_4$	3502	—498	372	(3487, 3517)	622
$\hat{N}_5$	3543	—452	364	(3534, 3562)	580
$\hat{N}_6$	3503	—497	546	(3482, 3524)	738

Table 11. *Negative ramp of mortality* ($a_i=b_i=1.0-0.005*i$).

a	b	c	d	e	f
$\hat{N}_1$	3914	—86	430	(3897, 3931)	439
$\hat{N}_2$	3917	—83	431	(3900, 3934)	439
$\hat{N}_3$	3864	—136	420	(3848, 3880)	441
$\hat{N}_4$	3901	—99	447	(3883, 3919)	458
$\hat{N}_5$	3914	—86	430	(3897, 3931)	439
$\hat{N}_6$	3747	—253	587	(3724, 3770)	639

Table 12. *Positive ramp of mortality* ($a_i=b_i=0.96+0.005*i$).

a	b	c	d	e	f
$\hat{N}_1$	3760	—240	402	(3744, 3776)	468
$\hat{N}_2$	3764	—236	403	(3748, 3780)	467
$\hat{N}_3$	3715	—285	392	(3700, 3730)	485
$\hat{N}_4$	3740	—260	415	(3724, 3756)	490
$\hat{N}_5$	3760	—240	402	(3744, 3776)	468
$\hat{N}_6$	3635	—365	565	(3613, 3657)	673

Table 13. *2 % of the unmarked individuals die between two subsequent samples, and 3 % of the marked:*

a	b	c	d	e	f
$\hat{N}_1$	3945	—57	436	(3926, 3960)	440
$\hat{N}_2$	3946	—54	437	(3929, 3963)	440
$\hat{N}_3$	3892	—108	425	(3875, 3909)	438
$\hat{N}_4$	3931	—69	452	(3913, 3949)	457
$\hat{N}_5$	3943	—57	436	(3926, 3960)	440
$\hat{N}_6$	3775	—225	593	(3752, 3798)	634

Table 14. *2 % of the unmarked individuals die between two subsequent samples, and 5 % of the marked:*

a	b	c	d	e	f
$\hat{N}_1$	4155	155	472	(4136, 4174)	497
$\hat{N}_2$	4156	156	473	(4137, 4175)	497
$\hat{N}_3$	4097	97	459	(4079, 4115)	469
$\hat{N}_4$	4155	155	493	(4136, 4174)	517
$\hat{N}_5$	4156	156	472	(4137, 4175)	497
$\hat{N}_6$	3932	—68	614	(3908, 3956)	618

Robustness against recruitment

Situations with recruitment were simulated with actual pipulation size N=4000 and 8 samples. Results:

Table 15. *2 % recruitment between two subsequent samples:*

a	b	c	d	e	f
$\tilde{N}_1$	4507	507	535	(4486, 4528)	737
$\tilde{N}_2$	4501	501	536	(4480, 4522)	734
$\tilde{N}_3$	4432	432	519	(4412, 4452)	675
$\tilde{N}_4$	4556	556	567	(4534, 4578)	794
$\tilde{N}_5$	4507	507	535	(4486, 4528)	737
$\tilde{N}_6$	4156	156	651	(4130, 4182)	669

Table 16. *4 % recruitment between two subsequent samples:*

a	b	c	d	e	f
$\tilde{N}_1$	5016	1016	635	(4991, 5041)	1198
$\tilde{N}_2$	5005	1005	636	(4980, 5030)	1189
$\tilde{N}_3$	4919	919	614	(4895, 4943)	1105
$\tilde{N}_4$	5127	1127	684	(5100, 5154)	1318
$\tilde{N}_5$	5017	1017	635	(4992, 5042)	1199
$\tilde{N}_6$	4511	511	706	(4483, 4539)	871

Table 17. *Negative ramp of recruitment* $(c_i=1.0—0.005*i)$:

a	b	c	d	e	f
$\tilde{N}_1$	4433	433	523	(4412, 4454)	679
$\tilde{N}_2$	4426	426	524	(4405, 4447)	675
$\tilde{N}_3$	4359	359	508	(4339, 4379)	622
$\tilde{N}_4$	4496	496	556	(4474, 4518)	745
$\tilde{N}_5$	4434	434	523	(4413, 4455)	680
$\tilde{N}_6$	4079	79	634	(4054, 4104)	639

Table 18. *Positive ramp of recruitment* $(c_i=0.96+0.005*i)$:

a	b	c	d	e	f
$\tilde{N}_1$	4577	577	547	(4556, 4598)	795
$\tilde{N}_2$	4574	574	548	(4553, 4595)	794
$\tilde{N}_3$	4502	502	531	(4481, 4523)	731
$\tilde{N}_4$	4615	615	547	(4595, 4635)	823
$\tilde{N}_5$	4578	578	547	(4557, 4599)	796
$\tilde{N}_6$	4233	233	671	(4207, 4259)	710

Robustness against migration

Situations where immigration and emigration were equal were simulated with actual population size N=4000 and 8 samples. Results:

Table 19. *1 % migration between two subsequent samples:*

a	b	c	d	e	f
$\tilde{N}_1$	4162	162	476	(4143, 4181)	503
$\tilde{N}_2$	4161	161	476	(4142, 4180)	502
$\tilde{N}_3$	4102	102	463	(4084, 4120)	474
$\tilde{N}_4$	4175	175	500	(4155, 4195)	530
$\tilde{N}_5$	4163	163	476	(4144, 4182)	503
$\tilde{N}_6$	3920	—80	611	(3896, 3944)	616

Table 20. *3 % migration between two subsequent samples:*

a	b	c	d	e	f
$\tilde{N}_1$	4437	437	521	(4417, 4457)	680
$\tilde{N}_2$	4433	433	522	(4413, 4453)	678
$\tilde{N}_3$	4366	366	506	(4346, 4386)	624
$\tilde{N}_4$	4471	471	551	(4449, 4493)	725
$\tilde{N}_5$	4437	437	521	(4417, 4457)	680
$\tilde{N}_6$	4117	117	644	(4092, 4142)	655

Table 21. *5 % migration between two subsequent samples:*

a	b	c	d	e	f
$\tilde{N}_1$	4714	714	572	(4692, 4736)	915
$\tilde{N}_2$	4708	708	573	(4686, 4730)	911
$\tilde{N}_3$	4632	632	555	(4610, 4654)	841
$\tilde{N}_4$	4771	771	607	(4747, 4795)	981
$\tilde{N}_5$	4714	714	572	(4692, 4736)	915
$\tilde{N}_6$	4317	317	678	(4290, 4344)	748

Table 22. *Negative ramp of migration* $(a_i=b_i=c_i=1.0—0.005*i)$:

a	b	c	d	e	f
$\tilde{N}_1$	4309	309	501	(4289, 4329)	589
$\tilde{N}_2$	4304	304	502	(4284, 4324)	587
$\tilde{N}_3$	4240	240	487	(4221, 4259)	543
$\tilde{N}_4$	4351	351	530	(4330, 4372)	636
$\tilde{N}_5$	4310	310	501	(4290, 4330)	589
$\tilde{N}_6$	3997	—3	621	(3973, 4021)	621

Table 23. *Positive ramp of migration* ($a_i=b_i=c_i=0.96+0.005*i$)*:*

a	b	c	d	e	f
$\hat{N}_1$	4277	277	496	(4257, 4297)	568
$\hat{N}_2$	4277	277	497	(4257, 4297)	569
$\hat{N}_3$	4214	214	482	(4195, 4233)	527
$\hat{N}_4$	4283	283	521	(4263, 4303)	593
$\hat{N}_5$	4278	278	496	(4258, 4298)	569
$\hat{N}_6$	4026	26	635	(4001, 4051)	636

Robustness against trap response

Situations with "differentiated catchability" and "trap shyness" were simulated with actual population size N=4000 and 8 samples. Results:

Table 24. *Differentiated catchability, K=1.05:*

a	b	c	d	e	f
$\hat{N}_1$	3844	—156	418	(3828, 3860)	446
$\hat{N}_2$	3844	—156	419	(3828, 3860)	447
$\hat{N}_3$	3793	—207	408	(3777, 3809)	458
$\hat{N}_4$	3847	—153	437	(3830, 3864)	463
$\hat{N}_5$	3844	—156	418	(3828, 3860)	446
$\hat{N}_6$	3657	—343	564	(3635, 3679)	660

Table 25. *Differentiated catchability, k=1.1:*

a	b	c	d	e	f
$\hat{N}_1$	3668	—332	387	(3653, 3683)	510
$\hat{N}_2$	3668	—332	388	(3653, 3683)	511
$\hat{N}_3$	3622	—378	379	(3607, 3637)	535
$\hat{N}_4$	3671	—329	405	(3655, 3687)	522
$\hat{N}_5$	3669	—331	387	(3654, 3684)	509
$\hat{N}_6$	3505	—495	533	(3484, 3526)	727

Table 26. *Trap shyness, k=0.95:*

a	b	c	d	e	f
$\hat{N}_1$	4253	253	491	(4234, 4272)	552
$\hat{N}_2$	4253	253	492	(4234, 4272)	553
$\hat{N}_3$	4191	191	477	(4172, 4210)	514
$\hat{N}_4$	4257	257	514	(4237, 4277)	575
$\hat{N}_5$	4253	253	491	(4234, 4272)	552
$\hat{N}_6$	4015	15	636	(3990, 4040)	636

Table 27. *Trap shyness, k=0.9:*

a	b	c	d	e	f
$\hat{N}_1$	4495	495	530	(4474, 4516)	725
$\hat{N}_2$	4495	495	531	(4474, 4516)	726
$\hat{N}_3$	4426	426	515	(4406, 4446)	668
$\hat{N}_4$	4499	499	555	(4477, 4521)	746
$\hat{N}_5$	4495	495	530	(4474, 4516)	725
$\hat{N}_6$	4219	219	669	(4193, 4245)	704

IV. DISCUSSION

From Tables 1—7 it can be seen that under ideal assumptions the estimate $\hat{N}_3$ is at least as accurate as any of the others in every situation simulated.

In simulated situations with equal mortality of marked and unmarked individuals, the estimate $\hat{N}_2$ is found to be at least as robust as any of the others (Tables 8—12). One should expect, however, that mortality is larger for marked individuals than for unmarked. From Tables 13—14 it can be seen that the estimate $\hat{N}_3$ is then at least as robust as any of the others in every situation simulated.

From Tables 15—23 it is clear that in situations with relatively small recruitment/migration the estimate $\hat{N}_3$ is at least as robust as any of the others in every situation simulated.

In simulated situations with differentiated catchability throughout the population being studied, the estimate $\hat{N}_1$ is found to be at least as robust as any of the others (Tables 24—25), and the difference in robustness between $\hat{N}_3$ and $\hat{N}_1$ is found to be relatively small.

In Tables 26—27 it can be seen that if marked individuals are generally less catchable than unmarked, the estimate $\hat{N}_3$ is at least as robust as any of the others in every situation simulated.

When a multiple marking experiment is carried out on a population, the magnitude of mortality, recruitment, migration and trap response occuring in the population during the sampling period is generally not known. The simulation results stated above thus strongly indicate that the estimate $\hat{N}_3$ should generally be preferred to $\hat{N}_1$, $\hat{N}_2$, $\hat{N}_4$, $\hat{N}_5$ and $\hat{N}_6$ when estimating population size from a multiple marking experiment with sample sizes about 100.

From Tables 8—12 it can be seen that the estimate $\hat{N}_3$ is most robust against mortality. If for instance 3 % of the population being studied die between each of two subsequent samples, 19 % of the population die during the sampling period, whilst from Table 9 it can be seen that the bias of $\hat{N}_3$ is then only 7 % of the actual population size, and that the standard deviation of $\hat{N}_3$ is less with 3 % mortality than under ideal conditions (Table 2).

Finally it may be of some academic interest to notice that in every situation simulated $\hat{N}_1$, $\hat{N}_2$ and $\hat{N}_5$ have almost identical bias and standard deviation.

V. SUMMARY

Six population estimates based on multiple marking were analysed by means of computer simulation. Results obtained in a multiple marking experiment on minnows in a small Norwegian lake were used as parameters in the simulations.

The bias and standard deviation of the estimates are examined, both when the underlying assumptions are valid and when they are not. In this way the accuracy of the estimates is analysed, as well as the robustness if mortality, recruitment, migration or trap response occur during the sampling period.

In every simulation carried out so that the underlying assumptions are valid, one of the most simple of these estimates (CHAPMAN's (1952) modification of SCHNABEL's (1938) estimate) is found to be at least as accurate as any of the others. This estimate is also found to be one of the most robust.

VI. ACKNOWLEDGMENT

My sincere thanks are due to LEIF LIEN, Zoological Museum, Oslo, for stimulating discussions of the problems at issue, and for letting me use his unpublished data on minnows as a base for the simulations.

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APPENDIX 1

Denote the left side of equation (1) by f(N), i.e.

$$f(N) = \sum_{i=2}^{s} \frac{(n_i - m_i)M_i}{N - M_i}$$

and let $l = \max\{i : 1 \leqslant i \leqslant s,\ n_i > m_i\}$. It is easily seen that $\lim_{N \to M_l^+} f(N) = \infty$, $\lim_{N \to \infty} f(N) = 0$ and that f(N) is monotone decreasing. Thus equation (1) has exactly one root.

Since $M_i \leqslant M_s$ for $i \leqslant s$,

$$\sum_{i=2}^{s} m_i = \sum_{i=2}^{s} \frac{(n_i - m_i)M_i}{\hat{N}_1 - M_i} \leqslant \frac{1}{\hat{N}_1 - M_s} \sum_{i=2}^{s} (n_i - m_i)M_i$$

i.e.
$$\hat{N}_1 \leqslant \frac{\sum_{i=2}^{s} (n_i - m_i)M_i}{\sum_{i=2}^{s} m_i} + M_s$$

Since $M_i > 0$ for $i \leqslant s$,

$$\sum_{i=2}^{s} m_i = \sum_{i=2}^{s} \frac{(n_i - m_i)M_i}{\hat{N}_1 - M_i} > \frac{1}{\hat{N}_1} \sum_{i=2}^{s} (n_i - m_i)M_i$$

i.e.
$$\hat{N}_1 > \frac{\sum_{i=2}^{s} (n_i - m_i)M_i}{\sum_{i=2}^{s} m_i}$$

APPENDIX 2

Equation (2) may be written

$$\sum_{i=1}^{s} \ln(1-n_i/N) = \ln(1-r/N) \tag{8}$$

Since $\ln(1-x) < -x$ when $0 < x < 1$, equation (8) implies that

$$\sum_{i=1}^{s} (-n_i/\hat{N}_5) > \ln(1-r/\hat{N}_5)$$

$$1-r/\hat{N}_5 < \exp\left(-\left(\sum_{i=1}^{s} n_i\right)/\hat{N}_5\right) \tag{9}$$

Since $e^{-x} < 1-x+\frac{1}{2}x^2$ when $x > 0$, the unequality (9) implies that

$$1-r/\hat{N}_5 < 1-\left(\sum_{i=1}^{s} n_i\right)/N_5+\frac{1}{2}\left(\sum_{i=1}^{s} n_i\right)^2/\hat{N}_5^2$$

i.e.

$$\hat{N}_5 < \frac{\left(\sum_{i=1}^{s} n_i\right)^2}{2\sum_{i=1}^{s} m_i}$$

Predator – Prey Relations Between Fish and Invertebrate Prey in Some Forest Lakes

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CONTENTS

I. INTRODUCTION

Within a study of the composition and distribution of zooplankton and benthos in relation to fish predation is, of course, analysis of the feeding habits of the fish populations of central importance. The purpose of the present investigation is to demonstrate the main directions of predation in two different types of fish populations, to discuss differences between the fish species in their degree of utilization of the food organisms, and also, to some extent, to discuss probable consequences for the prey species.

The feeding habits of the fish were followed in a group of small forest lakes with fundamental similarities in the abiotic conditions. For information about physical-chemical factors in lakes 1—8, see Stenson (1972, 1973). Occasional water analyses in lake no. 9 showed similarities between this lake and the others. The fish populations (initially similar in all lakes) are changed by means of a rotenone treatment in five of the lakes. The new populations consist of new species with significantly lower densities. The study started eight years after the treatment, *i.e.* enough time passed for the recovery of the invertebrate fauna. Samples were taken parallelly in the lakes, an arrangement which guaranteed sampling under similar environmental conditions.

II. THE FISH POPULATIONS

The fish species before and after the rotenone treatment are listed in Table 1. Some years after the rotenone treatment of lake no. 2, the original population (except perch) was restored during an extreme spring flood, when they managed to return through a ditch from another lake downstream.

Estimations of population density have been made on the basis of net fishing results, rotenone treatment data and input figures. Numbers shown in table are approximate (mean numbers for the investigation period), but they indicate well enough the density difference between the two types of lakes, thus helping to decide where the predation pressure is hardest. An idea about the reliability of the estimates is given by the results of a second rotenone treatment of lake no. 2 in November 1973. The estimated population density was 1,000 fish per ha, compared with the 1,300 fish per ha (678 fry and 642 yearlings and older) collected after the treatment. The under-estimation may be ascribed to difficulties in catching the smallest sizes of the population, with the methods used in this study.

Table 1. *Fish species before and after the rotenone treatment, estimations of population densities and gill net relations between perch and roach. One specimen of Tinca tinca was found after the second rotenone treatment of lake 2 in November 1973.*

Fish species	Lake No.												
	1	2		3	4		5		6	7		8	9
		*	†		*	†	*	†		*	†		*	†
Tinca tinca L.	—	+	+	—	—	—	—	—	—	—	—	—	—	—
Leuciscus rutilus (L.)	+	+	+	+	+	—	+	—	+	+	—	+	+	—
Perca fluviatilis L.	+	+	—	+	+	—	+	—	+	+	—	+	+	—
Esox lucius L.	+	+	+	—	—	—	+	—	+	+	—	—	+	—
Anguilla anguilla L.	+	+	+	+	+	—	+	—	+	+	—	+	+	—
Salmo trutta L.	—	—	—	—	—	—	—	+	—	—	+	—	—	+
Salmo gairdneri (RICHARDSON)	—	—	—	—	—	—	—	+	—	—	+	—	—	+
Salvelinus fontinalis (MITCHILL)	—	—	—	—	—	+	—	+	—	—	+	—	—	+
Estimated fish density (No./ha)	900		1000	900		75		125	900		125	900		125
Gill net relations between perch and roach	0.57			0.64					0.78			0.51		

* Before rotenone treatment

† After rotenone treatment

Table 1 also shows the numeric relations between perch and roach in the catches. Roach is more common than perch which may reflect a real difference in abundance in the lakes. This assumption is supported in other studies where roach is reported to be the dominating species, when perch and roach live sympatric under beneficial circumstances (*e.g.* SUMARI 1971).

The size and age distribution of fish are, besides the density, important for the intensity and direction of their predation. The original populations in lakes 1, 2, 3, 6 and 8, dominated by perch and roach, are spawning every year, which results in the production of large schools of fry. The salmonids in lakes 4, 5, 7 and 9 do not reproduce in these waters, and the populations are maintained by inputs of fish, most of which were more than one year old. There was no input in lakes 4 and 5 during the three years of stomach sampling. The numbers for lake 7 were: 46 per ha 1969; 32 per ha 1970; 23 per ha 1971. For lake 9 they were: 72 per ha 1969; 35 per ha 1970; 28 per ha 1971.

The fish fauna of the first lake type (lakes 1, 2, 3, 6 and 8) can be briefly characterized as a dense population with normal age distribution, and that of the second lake type (lakes 4, 5, 7 and 9) as a scarce population dominated by older fish.

III. MATERIAL AND METHODS

Fish sampling for stomach analyses was carried out in three different ways: (1) sport fishing, (2) gill net fishing and (3) cage trap fishing.

1. Stomachs (including oesophagus and gut) from sport fishing were collected in a box, which was placed in the study area. To each stomach was attached a form, completed by the fishermen, containing data about length, weight, species, lake no., date etc. This method gave stomachs mostly from the salmonid waters. Number of analysed salmonids is shown in Table 2.

2. Gill net fishing was carried out with a so called "survey net" (36 m long; 1.5 m deep; mesh sequence 75, 12.5, 33, 22, 43, 16.5, 30, 60, 38, 25, 10, and 50 mm). The net was exposed 1—4 hours depending on the water temperature. Fish were then carefully removed from the net and anesthetized (MS 222 SANDOZ): in order to make measurement (length and weight) and stomach flushing more easy. A rubber bulb with a plastic tube inserted was used to remove the stomach contents (SEABURG 1957). This method was only feasable on perch and salmonids in this investigation. It is, for anatomic reasons, difficult to empty the roach stomach by using this

Table 2. *Number of analysed salmonids in spring (March—April—May) summer (June—July—Aug.) and autumn (Sep.—Oct.). The majority of fish were in sizes 25—50 cm TL. Only 24 specimens were between 15—25 cm TL.*

	Brown trout				Rainbow trout				Brook trout
	Lake No.								
	5	7	9	Σ	5	7	9	Σ	4
Spring	7	23	29	59	8	13	30	51	3
Summer	18	21	78	117	9	13	41	63	9
Autumn	6	19	10	35	7	16	4	27	5

technique. In order to get material from roach, it was therefore necessary to take samples for dissection. Samples were drawn at random from each size class. Size classification, and number of analysed perch and roach in different size classes, are shown in Table 3. Fish who died in the net were, of course, analysed.

3. Cage traps of two types were used, those with wire netting (mesh 12.5 mm) and those with nylon netting (mesh 18.7 mm). Cages were exposed 2—6 hours. Fish were treated as above.

All stomachs and stomach contents were preserved in 4 % formalin. Food organism identification was, if possible, carried out to the species level, with some exceptions. In Diptera only Chironomidae was separated from other families, and terrestrial insects were classified to the order. Each stomach was assessed separately and the food items were counted. Insects were often damaged at ingestion and in such cases numbers were calculated by counting chitinous parts with species specific characters like head capsulae, mandibles, claws etc. The stomach contents of all individuals in each size class are treated as an unit in the tables.

Fish sampling must be carried out in a very careful manner in these small lakes with their limited fish populations, especially when the project is dealing with questions such as predation influence on plankton and benthos. When as in this case the effects of fish populations with different species and above all, differences in density, are investigated, it is of central importance that the denser population remain so during the

Table 3. *Number of analysed perch and roach on the three sample occasions (Size class I: < 10 cm; size class II: 10.0—14.9 cm; size class III: 15.0—19.9; size class IV: > 20 cm).*

		Perch					Roach					
		Lake No.										
Size class		1	3	6	8	Σ	1	2	3	6	8	Σ
Spring	I	6	3	2	3	14	5	4	7	3	5	24
	II	9	6	4	3	22	19	5	7	5	9	45
	III	5	—	1	—	6	8	13	11	6	8	46
	IV	—	—	1	—	1	1	—	2	2	10	15
Summer	I	5	8	4	4	21	4	7	4	—	—	15
	II	6	15	4	8	33	5	10	6	—	3	24
	III	6	5	3	3	17	3	5	6	—	3	17
	IV	3	2	2	1	8	—	4	—	—	5	9
Autumn	I	3	5	5	3	16	3	2	9	2	3	19
	II	8	7	9	6	30	6	3	16	6	7	38
	III	4	3	8	2	17	2	4	15	6	3	30
	IV	2	2	—	—	4	2	—	6	1	6	15

whole period of investigation. Intense fishing will probably cause changes in the fish fauna, which will result in changes in the predation pressure. An over-night operation with gill nets for example, would likely catch and kill at least 10 % of the fish population. There are consequently good reasons to restrict duration and number of fish sampling occasions at least in lakes with denser fish populations.

In order not to disturb the density relations between the lake types, fishing dates were chosen to get as much information as possible out of a minimized number of fishery strains. It was considered most relevant to study spring, summer, and fall conditions, *e.g.* seasons with fish feeding activities and a well developed invertebrate fauna. Gill net and cage trap fishing was carried out in July and September—October 1970, May, July and September 1971, and May 1972. Sport fishing gave stomachs during March—September 1969—1971.

IV. RESULTS

The food of the perch

Zooplankton

Planktonic crustaceans were prevalent in the diet of I—III sized fish on the three sample occasions. The relative importance (*i.e.* percentages of stomachs containing this food category) decreased with increasing fish size (Fig. 1). The perch fed mainly on copepods in the spring (*Heterocope appendiculata* G. O. SARS, *Eudiaptomus gracilis* G. O. SARS and *Cyclops* spp.), but also to a considerable extent on limnetic cladocerans (*Daphnia cristata* G. O. SARS and *Bosmina* spp.). The summer samples showed a more diversified plankton diet, probably as a result of the more diversified plankton picture in the lake. Limnetic species are still dominating among the cladocerans, and three new species turn up, *Diaphanosoma brachyurum* (LIEVEN), *Holopedium gibberum* ZADDACH and *Ceriodaphnia quadrangula* (O. F. MÜLLER). The diet now also includes several littoral species, living among weeds or benthic from the families Macrotricidae: *Drepanotrix dentata* (EURÉN) and *Acantholeberis curvirostris* (O. F. MÜLLER) Chydoridae: *Eurycercus lamellatus* (O. F. MÜLLER), *Acroperus harpae* BAIRD, *Alona* spp., *Alonella* spp., and Polyphemidae: *Polyphemus pediculus* L. This increase of the littoral species is more pronounced in the autumn, when *Ophryoxus gracilis* SARS is also present in the stimachs (Fig. 2 a—c). (The rotifer species *Asplanchna priodonta* and *Conochilus unicornis* were found in both perch and roach stomachs. The numbers were, however, impossible to estimate.)

Asellus

There is no clear tendency in the utilization of *Asellus aquaticus* (L.) as a food source over the three sample occasions. The relative importance, however, increases with increasing fish size (exclusive of size class IV).

Ephemeroptera

The number, as well as the relative importance of nymphs is highest in the spring stomachs and declines throughout summer to autumn. Spring stomachs include above all the species *Leptophlebia vespertina* (L), *L. marginata* (L.) and *Ephemera vulgata* L.. In the summer and autumn there is an addition of *Caenis* spp. and *Cloeon dipterum* (L.). The availibility for fish is probably correlated to the nymph activity in the free water, and predation increases when nymphs are leaving vegetation and sediment in order to emerge.

Odonata

Dragon fly nymphs occur in the food of fish from size class II and are most frequent in summer and autumn. Libellulidae nymphs are the most common and species such as *Cordulia aenea* L., *Somatochlora metallica* (VAN DER LIND) and *Libellula quadrimaculata* L. are present in approximately the same proportions. *Coenagrion puella* L. and *Erythromma najas* (HANSEM.) are the two Coenagriidae nymphs found in the stomachs.

Neuroptera

There is a relatively low utilization of *Sialis* larvae (fish in size class II—IV) on the three sample occasions. Relative importance seems to increase with increasing fish size.

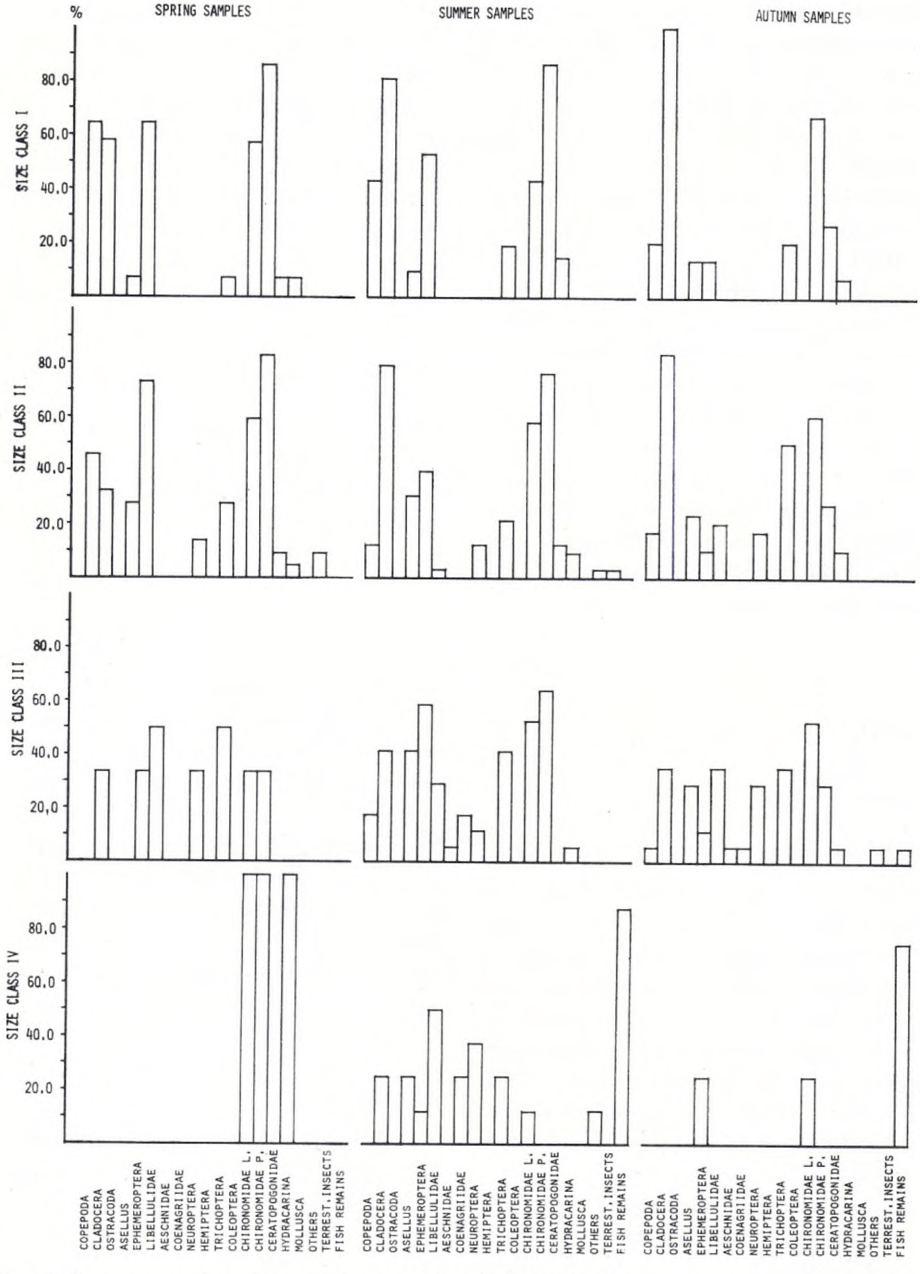

Fig. 1. Percentages of perch stomachs containing different food categories.

Trichoptera

The predation on caddis-fly larvae increases through spring and summer samples with maximum in the autumn. Relative importance grows with increasing fish size. Both net- and house-building species are present. *Cyrnus* spp., *Holocentropus* spp., *Phryganea striata* L., *Leptocerus aterrimus* Steph., *Limnophilus flavicornis* L. are in the diet in spring, summer and autumn samples, when *Molanna angustata* Curt. is also present.

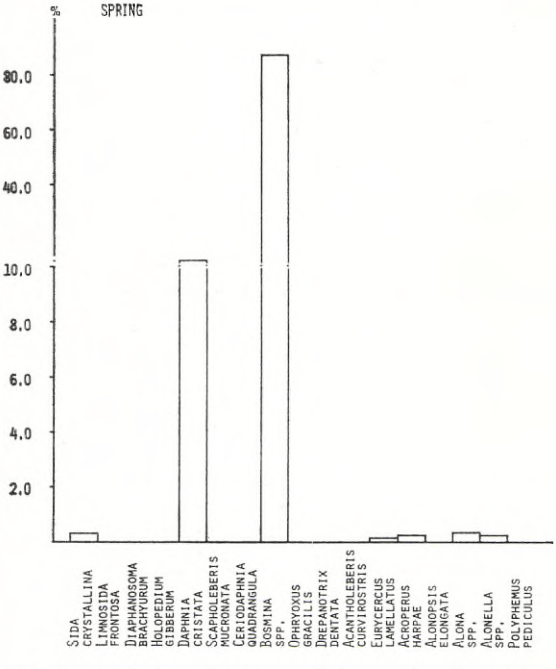

Fig. 2 a. Relations between Cladocera in the spring diet of perch.

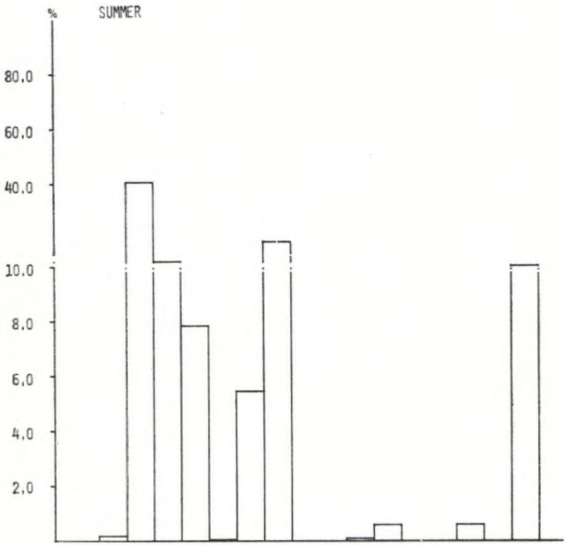

Fig. 2 b. Relations between Cladocera in the summer diet of perch.

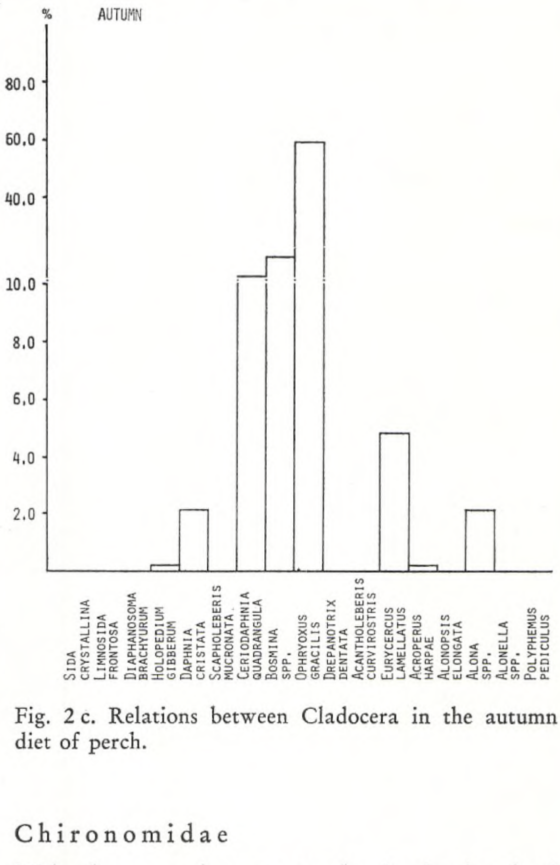

Fig. 2 c. Relations between Cladocera in the autumn diet of perch.

Chironomidae

Midge larvae and pupae are the dominating food objects among the benthic organisms. Pupae are most frequent in spring and summer samples, and the relative importance is also highest on these occasions. The situation is changed in the autumn to a dominance of larvae and a rising relative importance of these.

Vertebrate food

For fish in the largest size class invertebrate food organisms are loosing their importance and the perch changes to a fish diet. The majority of stomachs in this size class contained fish remains.

The picture given by the three sample occasions in this study agree with other investigations concerning the utilization of zooplankton, Ephemeroptera, Odonata and Trichoptera. Kjellberg (1971) and Craig (1974) show, moreover, the great importance of *Asellus aquaticus* through the winter and early spring, and also an early spring maximum of *Sialis* larvae. The choice of

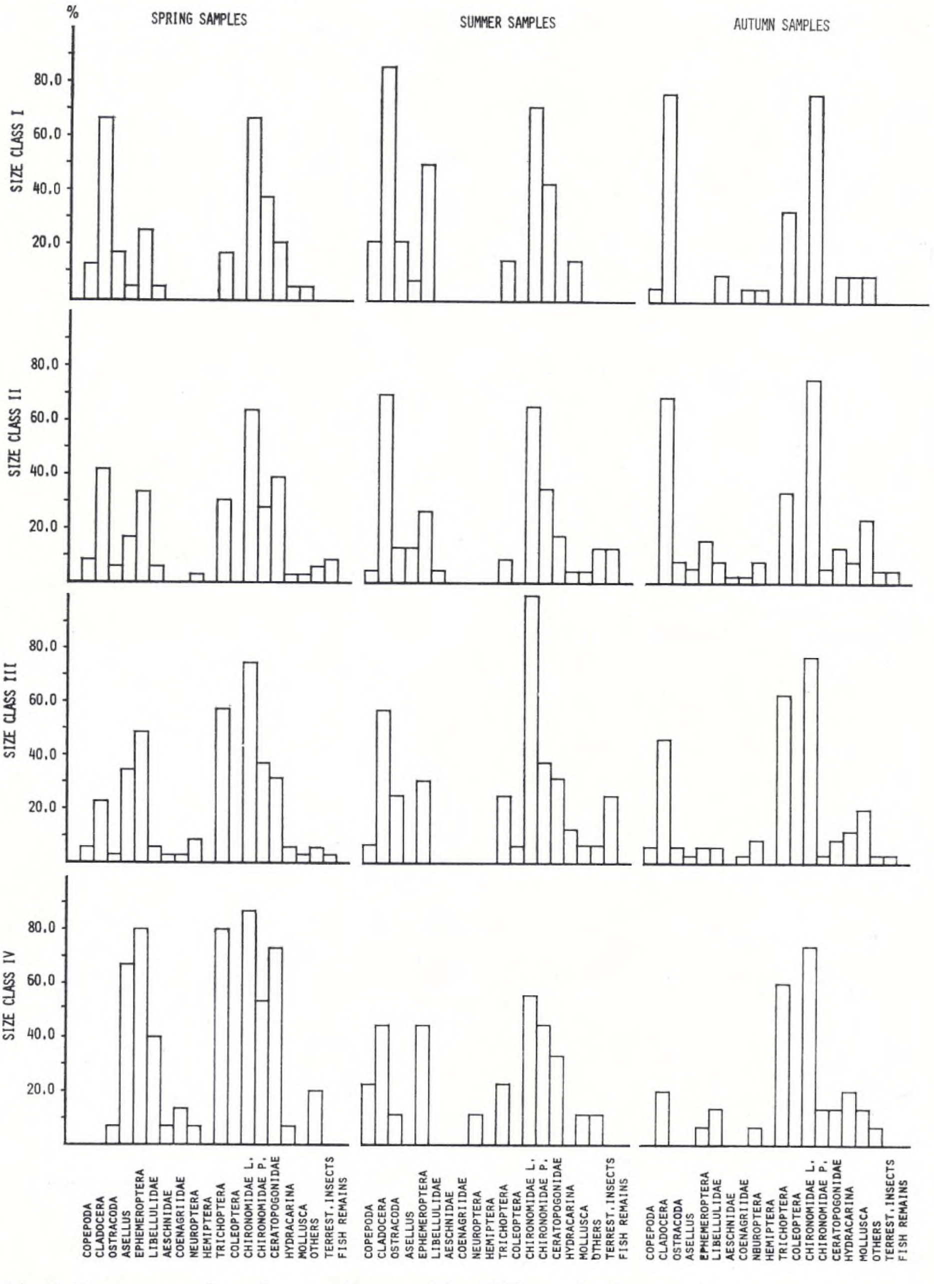

Fig. 3. Percentages of roach stomachs containing different food categories.

sample dates in this study may have resulted in the probable peak in *Asellus* and *Sialis* predation not being revealed.

The food of the roach

Roach subsist on both plant and animal food. Only the animal remains are quantitatively analysed. It may be noted that spring samples contained a good deal detritus, while summer and autumn stomachs contained algae especially filamentous. The animal part of the diet is, however, dominating in the great majority of the samples.

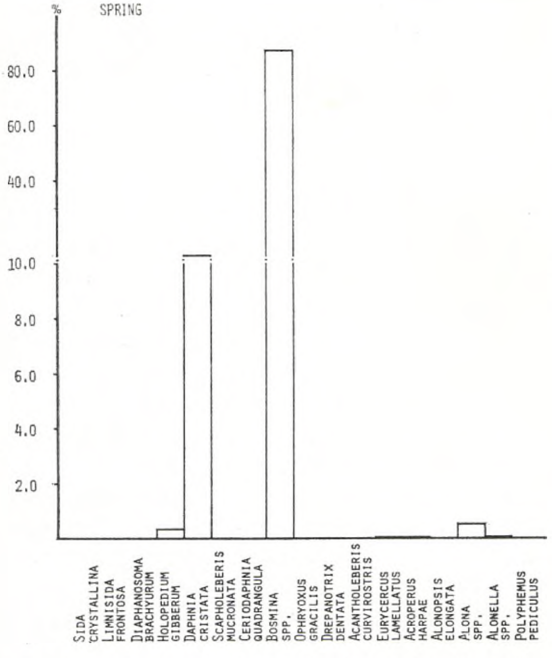

Fig. 4 a. Relations between Cladocera in the spring diet of roach.

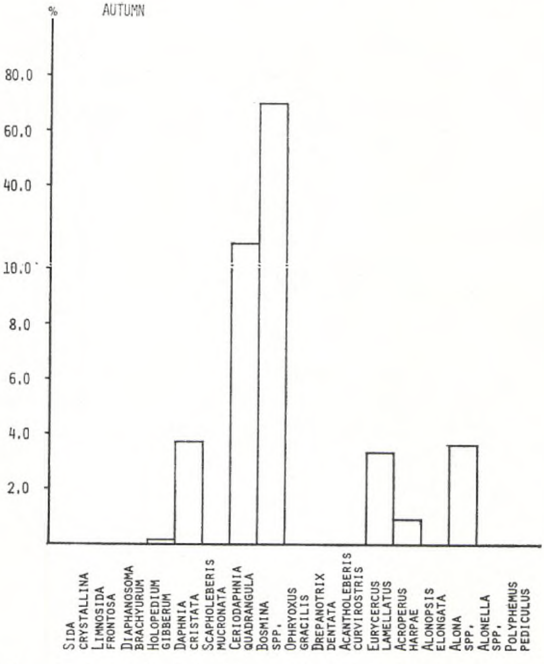

Fig. 4 c. Relations between Cladocera in the autumn diet of roach.

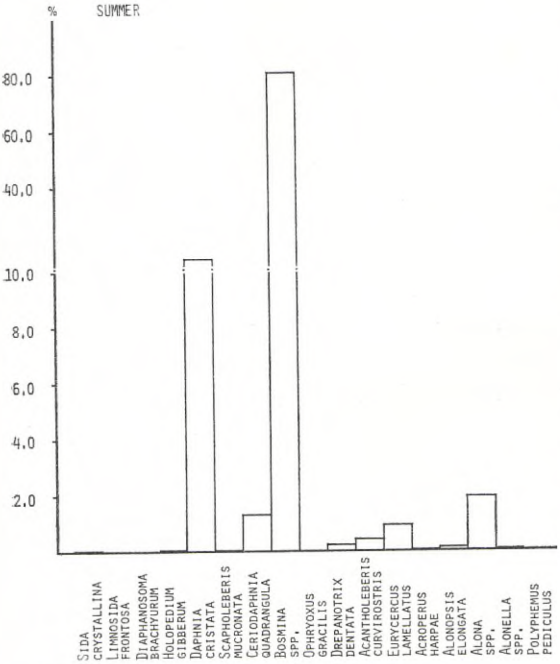

Fig. 4 b. Relations between Cladocera in the summer diet of roach.

Zooplankton

Planktonic crustaceans were most common in I—II sized fish. The relative importance is high up to size class III (Fig. 3). Copepods do not reach such high numbers as in the case of perch but are also most frequent in the spring and summer (mainly cyclopoids). Limnetic cladocerans are dominating. *Bosmina* spp. and *Daphnia cristata* are numerous in all samples with the addition of *Ceriodaphnia quadrangula* in summer and autumn. The share of littoral species increases in summer and autumn with *Drepanotrix dentata*, *Acantholeberis curvirostris*, *Eurycercus lamellatus*, *Acroperus harpae*, *Alonopsis elongata* SARS, *Alona* spp., and *Alonella* spp. (Fig. 4 a—c).

Another group of planktonic crustaceans present in the roach stomachs is Ostracoda. It seems to be relatively equal preyed upon over the year and the species present are *Candona candida* O. F. MÜLLER, *Cypria ophthalmica* Jurine and *Herpetocypris reptans* BAIRD.

Asellus

The number and also the relative importance of *Asellus aquaticus* is highest in the spring samples. It seems to be more important for roach in the larger size classes.

Ephemeroptera

Predation on may-fly nymphs is hardest in spring and summer, when relative importance is also greatest. The importance of this food category increases with increasing fish size. *Leptophlebia vespertina* and *L. marginata* dominate in the spring. Furthermore *Caenis* sp. and above all *Cloeon dipterum* appear in summer and autumn stomachs.

Odonata

Dragon fly nymphs have a low relative importance for roach. Libellulidae is the most frequent of the different families, and the same species are present here as in the perch food.

Neuroptera

Sialis larvae occur in low numbers in all size classes. The importance seems, however, to increase with increasing fish size.

Trichoptera

The number of caddis-fly larvae is highest in the spring and autumn. The relative importance, with peaks in spring and autumn, rises with increasing fish size. The species composition and appearance in the food is the same as for perch with the addition of *Mystacides longicornis* L. and *Oxyethira flavicornis* CURT.

Chironomidae

Midge larvae and pupae are the dominating food objects among the benthic animals. Larvae show both high numbers and great relative imporortance on all sample occasions. Pupae are included to a lesser extent with the exception of summer samples of size class IV.

Ceratopogonidae

Another dipteran family with significantly high numbers in spring and summer stomachs is Ceratopogonidae. The larvae live predatory on other gnat larvae. They probably occur together with chironomids in or on the sediment, and are eaten together with these.

Mollusca

Pisidium spp. occur in all size classes with a maximum in the autumn. *Pisidium* is the only genus in the diet although there are several others present in the lakes.

The dietary habits of roach have been reviewed in many papers. The general information is that stomach content is quite variable. KJELLBERG (op.cit.), who also described the food habits in a nutrient-poor lake, showed prevalence of animal matter during the period spring—summer—autumn. The proportion of vegetable matters tends to increase in eutrophic lakes and streams (ALM 1922, HARTLEY 1947, 1948, HYNES 1950, GRAF VON WESTPHALEN 1956, STANGENBERG 1958). Increase of vegetation in the food is correlated to shortage of animal food objects according to LYAGINA (1972).

The food of the salmonids

Brown trout, rainbow trout and brook trout are treated together in the text, because of the great similarities in the food composition and the importance of different food categories. The picture of brook trout food is by no means complete because of too few samples, but the species composition in the diet agree with those of the other two species. The description in the text is also applicable to the small material of brown and rainbow trout in sizes under 25 cm. The different species are treated separately in figures and tables.

Zooplankton

Planktonic crustaceans are of secondary importance in the diet, and occur in the stomachs during a relatively short period (mid-June—mid-September). Only the larger species *Holopedium gibberum*, *Daphnia longispina* O. F. MÜLLER, *Eurycercus lamellatus* and *Bythotrephes longimanus* LEYDIG are subjected to predation (Figs. 5 and 6).

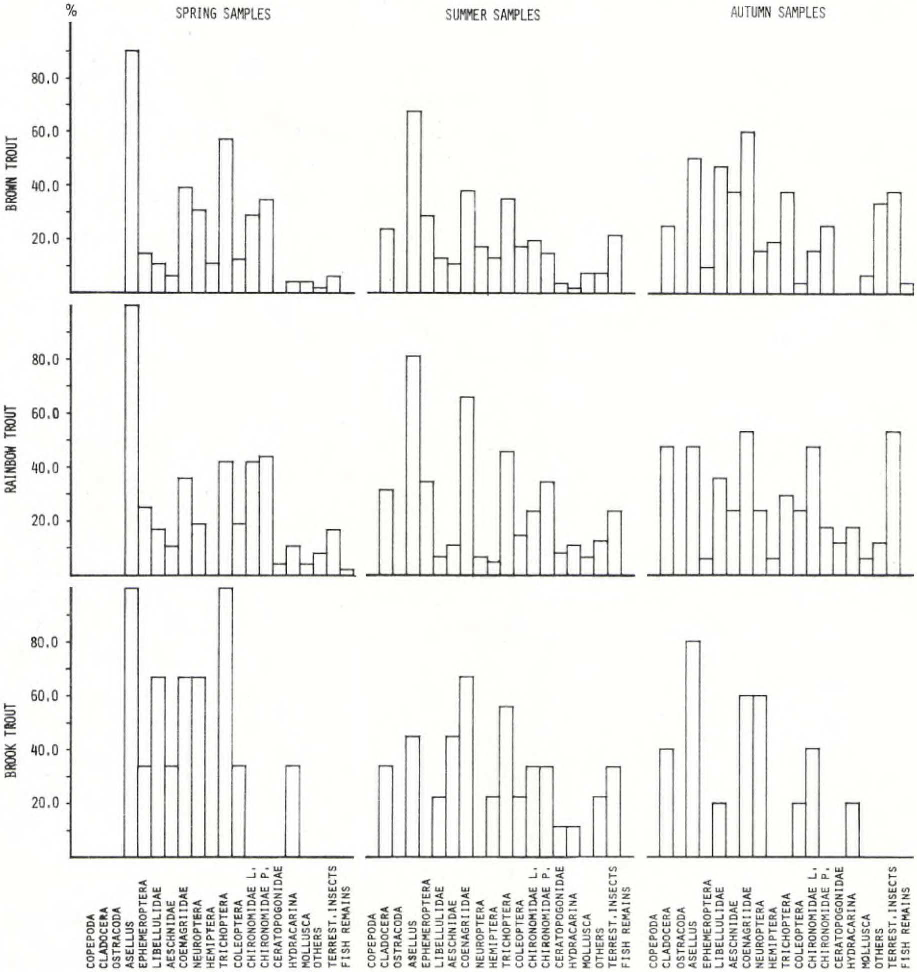

Fig. 5. Percentages of salmonid stomachs containing different food categories.

Asellus

The water slater forms a basic food source during the year, with highest relative importance in the spring.

Ephemeroptera

Predation on may-flies reaches its highest level and relative importance in spring and summer. Nymphs of *Ephemera vulgata*, *Leptophlebia vespertina*, *L. marginata* are prevalent in the spring diet, but in late May and during June, there is an increase in importance of sub-imagines of emerging *Ephemera vulgata*. *Cloeon dipterum* in addition to nymphs of the species already mentioned, occurs in summer and autumn stomachs.

Odonata

All three families are utilized to a high degree. Relative importance tends to increase towards autumn.

Libellulidae: nymphs of *Cordulia aenea*, *Sympetrum vulgatum* L. and *Libellula quadrimaculata* occur in spring samples. From June on imagines turn up and the occurence in the stomachs reflect emergence occasions of the different species. (*Cordulia aenae* mid-Jun—mid-Jul; *Sympetrum vulgatum* late-Jul—mid-Sep; *Libellula quadrimaculata* mid-Jun—mid-Sep). Nymphs are present between and after the main emergences. Dragon flies are evidently subjected to an intensive predation at the time of their final moult. The nymph

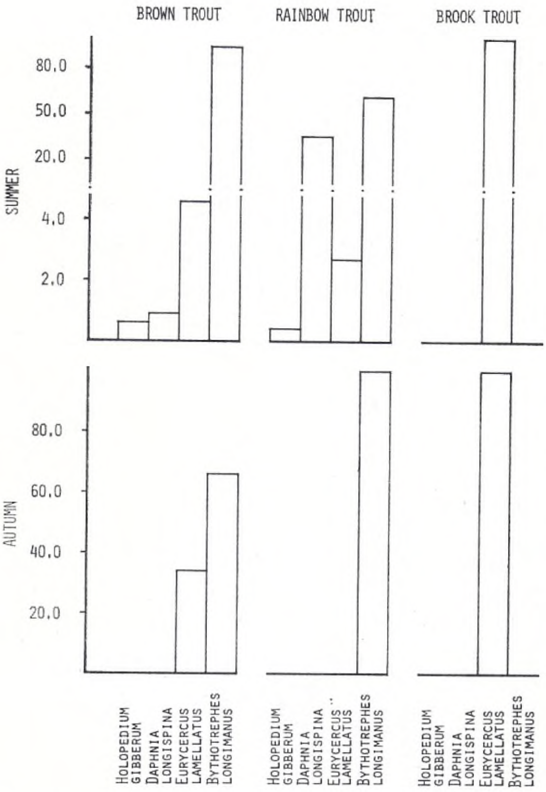

Fig. 6. Percentage relations between Cladocera in the summer and autumn diet of the salmonids.

climbs up a water plant out of the water, where the newly emerged dragon fly is exposed to fish during the expansion phase of the wings. Aeschnidae: nymphs are frequent in spring, early summer and autumn. Adults are present throughout summer and early autumn. Coenagriidae: Both nymphs and adults are heavily preyed upon with high values of relative importance. Nymphs of *Coenagrion* spp. (*C. puella C. armatum* CHARP.), *Enallagma cyathigerum* CHARP., *Erythromma najas* are frequent in the spring. The species are, as adults later in the summer, of primary importance in the diet. Imagines of *Enallagma cyathigerum*, *Erythromma najas* and *Lestes sponsa* occur from June—September, while at the same time nymphs of several species are present (*i.a. Coenagrion* spp. and *Ischnura elegans* LIND).

Neuroptera

Sialis lutaria L. larvae are in the diet during the whole sampling period, with highest relative importance in the spring.

Hemiptera

Water bugs of the families Gerridae (*Gerris najas* DEG.), Notonectidae (*Notonecta glauca* L.) and above all Corixidae are found in the stomachs at all seasons.

Trichoptera

Larvae, especially of house building species, are eaten in great numbers, with highest relative importance in the spring. *Phryganea striata* L., *P. varia* FABR., *P. grandis* L., *P. obsoleta* MAC.-LACHL., *Limnophilus flavicornis*, L. and *Leptocerus aterrimus* are frequent in the beginning of the year. Larvae of *Mystacides nigra* L., *M. azurea* L., *Limnophilus rhombicus* L. and *Molanna angustata* are added in the summer, when also imagines of *Phryganea varia* and *Leptocerus aterrimus* occur. *Phryganea* spp. and Cyrnus spp. larvae are the dominating species in the autumn diet.

Coleoptera

Only imagines of the beetles are found in the stomachs. Most frequent are diving species such as *Dytiscus marginalis* L., *Laccophilus hyalinus* DEG. and *Platambus maculatus* L. but also more or less surface living species as *Gyrinus natator* L., *Donacia* sp. and *Galerucella nymphaea* L. are common.

Chironomidae

Midge larvae and pupae are utilized during the whole sampling period, with highest relative importance in spring stomachs. One interesting point is that both larvae and pupae seem to be of greater significance in the smaller lakes 5 and 7 than in the larger lake 9.

Terrestrial food

Hemiptera, Coleoptera and above all Hymenoptera (Formicidae: *Formica rufa* L. and *Camponotus herculeanus* L.) are of high relative importance

Table 4. *The percentage distribution of limnetic and littoral Cladocera in perch and roach food. (Limnetic species: Diaphanosoma brachyurum, Holopedium gibberum, Daphnia cristata, Ceriodaphnia quadrangula, Bosmina spp.*; Littoral species: *Sida crystallina, Limnosida frontosa, Scapholeberis mucronata, Ophryoxus gracilis, Drepanotrix dentata, Acantholeberis curvirostris, Acroperus harpae, Alonopsis elongata, Alona* spp., *Alonella* spp., *Polyphemus pediculus.)*

	Perch		Roach		Roach in lake No. 2	
	Limnetic species	Littoral species	Limnetic species	Littoral species	Limnetic species	Littoral species
Spring	98.7	1.3	99.4	0.6	0	100
Summer	87.6	12.4	96.5	3.5	2.6	97.4
Autumn	34.2	65.8	92.3	7.7	11.1	88.9

in summer and fall diet. Swarming ants drowned in the water are easy prey for the fish and are sometimes numerous in the stomachs.

Vertebrate food

Objects of vertebrate origin are very rare in the stomachs. Fish occurred only three times in lakes where we have had an input of small fish during the sampling period. Remains of smooth newts (*Triturus vulgaris* L.) and frogs (*Rana* sp.) were found in four stomachs and one brown trout contained a vole (*Microtus* sp.).

The feeding habits of salmonids, introduced in rotenone-treated waters, seem to be quite varied, depending on the abundance of different food species. Many reports show the great importance of benthic organisms. *Asellus aquaticus* is an example of a species which often dominates the spring and early summer diet, while nymphs and adults of aquatic insects especially Odonata prevail in late summer and autumn. The three trout species (brown, rainbow and brook trout) show great similarities, even when they live together, at low or moderate densities, in the same lake (BERGLUND 1968; KJELLBERG 1969; TUUNAINEN 1970).

V. DISCUSSION

Comparison of the food of perch and roach

The diet of the two species shows several similarities. The smaller fish size classes subsist on planktonic crustaceans, and with increasing fish size there is a gradual transition taking place, towards an increasing intermixing of benthic organisms.

After a more detailed analysis of the food, not only restricted to a rough categorization on order or family level, much more information is given. Besides the differences concerning the copepode utilization, an examination of the cladoceran species in the stomachs points to certain differences. The percentages of limnetic and littoral cladocerans eaten on the three sample occasions are shown in Table 4. Limnetic species are dominating in the roach food, with a minor increase of littoral species towards autumn. This increase is more pronounced in the perch stomachs, where littoral species prevail in the autumn. Both species prey on small-sized genera as *e.g. Bosmina* and *Ceriodaphnia.* A comparison between the mean size of *Bosmina* spp. from stomachs of sympatrically living perch and roach (lake 3, size class II), reveals a significantly lower size in the roach diet ($p < 0.00003$, MANN-WHITNEY U-test) (Fig. 7). This indicates a greater ability of roach to prey on even smaller zooplankton than perch, which may be more competitive when resources are limited. The information above may indicate the existence of some kind of interactive segregation between the species in their food selection. Studies made on these and related problems show that differences between species do not need to be obvious or exist at all, when food is superabundant, but the magnitude of differences tends to increase when competition between species is intensified, in one way or another (SVÄRDSON

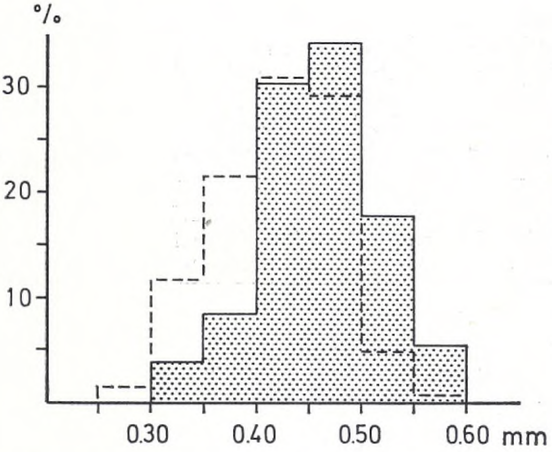

Fig. 7. Size distribution of *Bosmina spp.* within stomachs of sympatrically living perch and roach (size class II, lake 3). Dotted distribution — perch.

1949, Lindroth 1955, Kalleberg 1958, Nilsson 1963, 1965, 1967, 1972). Ivlev (1961) showed by experiment how the presence of competing species caused a change in the preferred food. The question, raised by the results in Table 4, is whether or not the distribution of cladocerans in perch and roach diet is influenced by competition. In other words is competition contributing to the realization of their food niches? A positive answer may be supported by the results from lake no. 2, where roach, in the absence of perch, fed mainly on littoral species. Also copopods were more frequent in the roch stomachs from this lake (14.0 % contained copepods compared to 4.6 % in the other lakes). These results, however, must not be so unambigously interpreted. We must consider also factors other than the lack of interspecific competition between roach and perch. The rarity of limnetic species in the roach stomachs from this lake may also be ascribed to a decreasing attractivity following the low mean size of the limnetic species (Stenson 1972), a situation which may be caused by more intensive predation from the denser fish population in this lake. The nature of these questions is very complex. Data, which can be used to approach the solution, are now being gathered as part of a field experiment, where a perch population is to be introduced into a lake with a roach population.

There were, on the whole, similarities in the predation on benthos, but besides some minor differences in the utilization of Ephemeroptera, Odonata and Trichoptera (see above), there are more basic differences. The relation between chironomide larvae and pupae in the stomachs, indicates a more active search at the bottom in the sediment by roach. This is also supported by the fact that sediment-dwelling mussels (*Pisidium* spp.) are found exclusively in the roach diet.

To summarize: roach seems on the whole to utilize a broader spectrum of animal food species and roach can better than perch prey on small-sized limnetic zooplankton. Moreover roach is obviously capable to feed directly on the primary producers, a food source which is inaccessible to perch.

Comparison of perch-roach diet and salmonid diet

The differences in predation on zooplankton are strikingly evident for the two fish population types, when we look at the tables and figures. (Information about the total number of organisms in different food categories found in the stomachs of perch, roach and salmonids, is given in Table 5). Perch and roach prey upon a large number of species of Copepoda as well as Cladocera from spring to autumn, while the salmonids do this only during a shorter period and utilize a few large species as a food source. We are able to realize the ecological consequences for the plankton communities when we also consider, firstly the differences in density (Table 1) and structure of the fish populations, and secondly the prey selecting strategy of the fish. The significantly denser perch and roach populations consisting of fish in all size classes, exert a hard predation pressure which acts in a size-selective way on the zooplankton. Data in Stenson (1972, 1973, 1976) illustrate the effects on cladocerans. Their mean size is lower in perch and roach lakes, where larger species are either absent or present in lower abundance with a lower mean size. *Daphnia longispina* and *Bythotrephes longimanus* are not found in high predation lakes and *Holopedium gibberum* is here present in lower abundance with lower mean length. The larger *Bosmina coregoni* is more heavily preyed upon than the smaller *B. longirostris*, a fact which probably influences the numeric relations between the two species.

Table 5. *Total number of organisms in different food categories found in the stomachs of perch, roach and salmonids.*

	Perch					Roach					Brown trout	Rainbow trout	Brook trout
	Size class												
Food Category	I	II	III	IV	Σ	I	II	III	IV	Σ			
Copepoda	714	3452	847	0	5013	29	448	8	10	495	0	0	0
Cladocera	5293	5484	527	3	11307	11754	8412	203	28	20397	2837	3049	24
Ostracoda	0	0	0	0	0	15	11	10	2	38	0	0	0
Asellus	5	51	45	9	110	2	18	30	45	95	12643	11732	372
Ephemeroptera	55	155	42	4	256	31	59	169	1025	1284	610	256	2
Libellulidae	0	9	25	6	40	4	6	11	30	51	86	29	8
Aeschnidae	0	0	3	0	3	0	1	1	1	3	71	23	15
Coenagriidae	0	0	4	3	7	0	1	2	3	6	1133	569	190
Neuroptera	0	17	18	5	40	1	4	12	6	23	116	28	19
Hemiptera	0	0	0	0	0	0	0	0	0	0	116	25	8
Trichoptera	10	57	47	6	120	23	72	172	99	366	405	711	32
Coleoptera	0	0	0	0	0	0	0	1	0	1	39	30	13
Chironomidae l.	169	602	184	10	965	825	1644	2362	954	5785	158	142	9
Chironomidae p.	400	951	338	147	1863	48	92	133	883	1106	2521	1084	11
Ceratopogonidae	8	20	1	0	29	18	121	140	252	531	3	11	1
Hydracarina	1	28	4	1	34	6	7	20	5	38	5	59	3
Mollusca	0	0	0	0	0	12	111	238	54	415	23	13	0
Others	0	4	5	1	10	0	8	8	9	25	75	70	25
Terrest. insects	0	1	0	0	1	1	41	23	0	65	806	160	8
Fish remains	0	0	0	11	11	0	0	0	0	0	2	1	0

Table 6. *Frequency of bottom samples with and without Odonata, Asellus aquaticus and Ephemeroptera. Samples were taken with an* Ekman-*sampler on 2—3 m depth in the littoral zone. This part of the littoral zone is well exposed for fish predation, and any effects of differential predation from the two fish population types may be revealed in this zone.*

Year	Perch-Roach lakes		Salmonid lakes		χ^2	p
	samples with	samples without	samples with	samples without		
Odonata						
1969	3	27	12	6	16.81	< 0.05
1970	4	26	8	10	5.81	< 0.05
1971	5	55	12	24	9.65	< 0.05
Asellus						
1969	13	17	15	3	7.41	< 0.05
1970	10	20	17	1	17.07	< 0.05
1971	30	30	31	5	12.67	< 0.05
Ephemeroptera						
1969	29	1	14	4	4.30	< 0.05
1970	29	1	12	6	8.13	< 0.05
1971	56	4	20	16	19.47	< 0.05

Several differences are obvious, when the stomach contents of the two fish populations are compared with special attention to larger invertebrate organisms. Certain groups (such as aquatic Hemiptera and Coleoptera) are found almost only in the salmonid stomachs. *Asellus aquaticus* is more frequent in the salmonid diet where also Odonata and Trichoptera are represented by a larger number of species. Can this be explained by a higher efficiency by salmonids in catching these animals or is the occurrence in the stomachs reflecting differences in abundance between the lakes?

In order to answer this question properly, it is necessary to have more information about the food searching strategy of the different fish species when they live under similar food conditions, and about the abundance and distribution of these food categories in the lakes.

In lakes with a small fish population like the salmonid waters in this study, where population size is determined by factors other than food shortage, food organisms can be superabundant. It is under these circumstances possible for food species, even those which are more susceptible to predation, to co-exist with fish during periods of varying length. A low utilization degree is tolerable from the prey's point of view, and their abundance and distribution within the lakes is not too dramatically influenced. A situation with low predation pressure may, in cases of species with aquatic larval stages, imply a higher probability for them to reach emergence or metamorphosis.

A dramatic increase in the pressure from predators may give the following effects. A decrease of the most susceptible prey species will occur in areas where they are exposed to fish. (This could be expressed as a decline of the frequence of these species in the fish stomachs.) The distribution of these groups will be restricted to the margins of the lakes.

Is it so that *Asellus*, the aquatic Hemiptera and Coleoptera and those dragon fly and caddis fly species which occurred mostly in the salmonid diet, are so susceptible to predation that they are more or less excluded from "fish areas" in the perch and roach lakes, where a harder predation pressure prevails? There is some evidence for their lower abundance in the perch and roach lakes. The frequency of samples with *Asellus* and

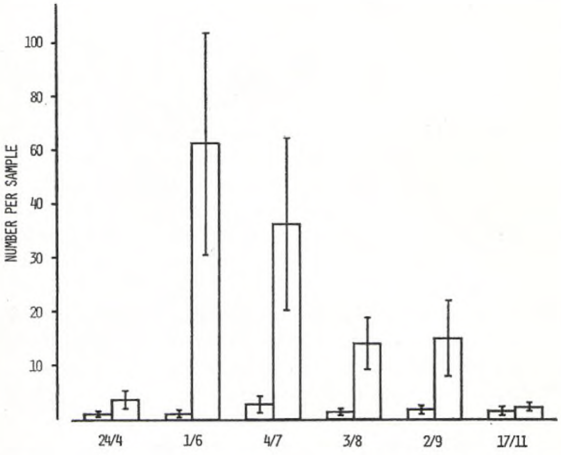

Fig. 8. Number and SE (standard error) of *Asellus aquaticus* per Ekman sample. 10 samples were taken in the perch and roach lakes and 6 samples were taken in the salmonid lakes each date. Left bars — perch and roach lakes, right bars — salmonid lakes.

dragon fly nymphs was higher in the outer littoral zone (2—3 m; well exposed for fish predation) in the salmonid lakes than in the perch roach lakes (Table 6). The difference is significant over the three years of sampling ($p < 0.05$, χ^2 — test). Also the abundance of *Asellus* in this special bottom zone differs between the two lake types with significantly higher means in the salmonid lakes from early summer to fall ($p < 0.05$, MANN-WHITNEY U-test) (Fig. 8). In a study on littoral "active fauna" carried out in lakes 2, 3, 4, 5 and 7, Corixidae was found only in samples from the salmonid lakes 4, 5, and 7 (ERIKSSON 1974). Abundance increase of these organisms is obvious in lakes, where the fish populations have been reduced by means of rotenone or as a result of acidification. So is *e.g.* Corixidae now numerous in lake 2, after a rotenone treatment which eliminated the fish population in 1973. HENRIKSON and OSCARSON (1978) showed that the recent colonization by the corixid species *Glaenocorixa propinqua* (FIEB.) of many of the acidified lakes in southwestern Sweden is correlated to the decrease in these lakes of predation pressure from fish. This close connection between abundance and distribution of *e.g.* Hemiptera and predation from fish is also demonstrated by MACAN (1965, 1966 a, 1966 b) in the study on the effects of the fish introduction into Hodsons Tarn. Berglund (1968) showed that *Asellus aquaticus* declined when predation pressure from fish increased. Abundance of *Lepidurus arcticus* PALLAS is obviously affected by fish predation according to AASS (1969). SVÄRDSON (1972) showed that populations of crayfish (*Astacus astacus* L.) declined in localities where the eel population (*Anguilla anguilla* L.) increased.

Diet analyses of a perch population introduced in a lake previously without fish show that large insects, larvae and imagines, are the most common food objects. This indicates that perch have a food searching strategy, similar to that of the salmonids, when perch is living under superabundant food conditions (HENRIKSON and OSCARSON 1978).

Final remarks

From the data and discussion above we can conclude that fish prey on benthic and "active fauna" in a selective way. Primary effects of this selection are reduction in numbers and an affected spatial distribution of these susceptible groups (*e.g. Asellus*, Odonata, aquatic Hemiptera). Are there also secondary effects of this selective fish feeding? Does for example the selection for dragon fly nymphs imply a decreasing pressure on their prey organisms resulting in higher abundance of these? The higher frequency of samples with May-fly nymphs from the perch and roach lakes (Table 6) may in fact be an indication of a lower pressure from the less frequent dragon fly nymphs in this lake type.

Although there is evidence for a predatory influence on abundance and distribution of benthic and "active fauna" animals, a more detailed analysis of the consequences of fish selectivity is required before the question can be answered whether fish predation can have a correspondingly strong influence on structure and function within the benthic fauna and "active fauna" as it does on zooplankton.

VI. SUMMARY

1. The feeding habits of two types of fish populations, with differences in species composition and density, were examined.

2. Perch and roach utilized crustacean zooplankton to a significantly higher degree and during a longer period than the salmonids. Only larger species occurred in the salmonid stomachs.

3. Copepoda and littoral Cladocera were more frequent in the perch stomachs than in the roach.

4. Roach stomachs contained significantly smaller *Bosmina* spp. than perch stomachs, when fish of the same size were compared.

5. Ostracods were found only in the roach stomachs.

6. Roach search more than perch in and on the bottom sediment as seen by the greater importance of Chironomidae larvae, Ceratopogonidae larvae and *Pisidium* spp. in the roach stomachs.

7. The larger number of *Asellus aquaticus*, Trichoptera and Odonata species, the higher frequence of emerging specimens and the regularly presence of aquatic Hemiptera and Coleoptera in the salmonid diet, when compared to the perch and roach diet, indicate a predatory influence on the spatial distribution and abundance of these groups. This predatory influence is also revealed in bottom samples, where *Asellus* and dragon fly nymphs are more common in the salmonid lakes where the lowest predation pressure from fish prevails.

8. The selection for invertebrate predators (*e.g.* dragon fly nymphs) may change the balance and numeric relations between predators and prey in the benthic community.

VII. ACKNOWLEDGMENTS

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The Body/Scale Relationship in Roach, *Rutilus rutilus* (L.), from a Baltic Archipelago

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CONTENTS

I. INTRODUCTION

In order to make possible the use of the distances between annuli on fish scales for back-calculating growth, mathematical models are employed to describe the relation of these models between scale and body lengths. The simplest of these, $y=a+bx$, with $a=0$, was tried by DAHL (1910) and LEA (1910) and, with $a\neq0$, by LEE 1912. For species with a non-linear body/scale relationship other models have to be used. SHERIFF (1922) tried a polynomial of the second order on herring. MONASTYRSKY (1930) used an exponential function on roach and some other species. His model has since been tested on roach by FRANK (1959, 1962), among others, and also on other species, *e.g.* perch (*operculum*), by LE CREN (1947) and AGNEDAL (1968). SEGERSTRÅLE (1933) successfully used empirically derived body/scale curves without, however, attempting to give them a mathematical form. In this paper, mathematical models mentioned above have been tested on the body/scale relationship in roach, *Rutilus rutilus* (L.) The principal aim has been to arrive at a formula for use in automatic processing of growth data. This has not necessitated absolute statistical stringency in all respects.

II. MATERIAL AND METHODS

The roaches were sampled from a Baltic archipelago area, Marviken, 110 km south-west of Stockholm. The mean salinity in the area is about 6 ‰. Adult fish were caught with gill nets and juveniles by blasting with dynamite. About 1,100 females were arranged in length groups with a class width of 20 mm from 40 mm to 260 mm (total lengths), 100 in each group. The smallest fish had a length of 51 mm. About ten scales were removed from each fish from an area below the lateral line on the left side of the body (Fig. 1) and placed between two ordinary microscope slides. The lengths of six of these scales were measured in a microscope with an ocular micrometer. The length was measured as the radius that runs obliquely backwards and upwards from the focus (Fig. 1). In most cases a fissure here forms a radius. The "caudo-dorsal" radius was chosen as being the one along which the annuli are easiest to identify. Scales with resorbed margins were excluded. The scales were measured with an accuracy of 0.025 mm and the body length was registered in millimetres. The data were processed by computer.

As mentioned above, the smallest fish in the sample had a length of 51 mm. In the investigation area, however, the roach normally reaches a length of 35—45 mm during the first year. This means that the sample did not include the first

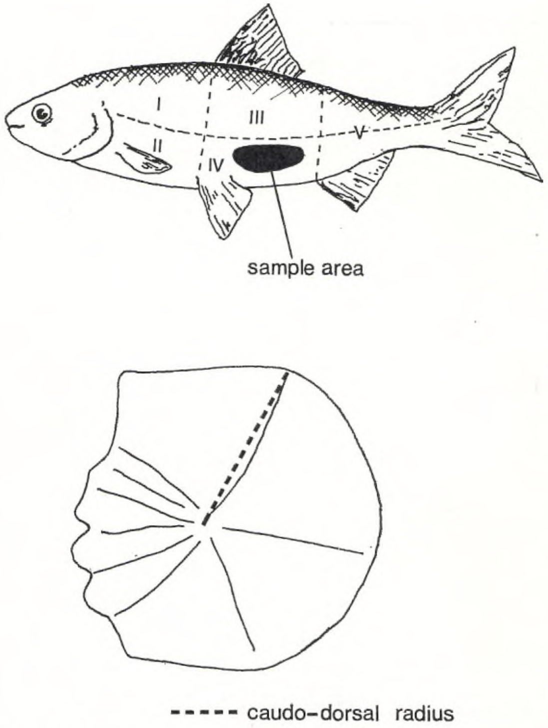


Fig. 1. Sample area and measured radius of the scales.

year. In order to compensate for this deficiency, the body/scale relationship was investigated for a sample of 130 formalin-fixed roaches from Simpevarp, an archipelago area 130 km south of Marviken. These fishes were caught after the growing season, mostly in November, during the period 1970—76. This material was not included in the main sample because of the deviating sampling technique.

III. RESULTS

Models

As has been mentioned in the Introduction, three models for the body/scale relationship were tested. They have the following forms:

$Y_i = \alpha + \beta X_i + \varepsilon_i$ (1)
$Y_i = \alpha + \beta_1 X_{1i} + \beta_2 X_{2i} + \beta_3 X_{3i} + \ldots \varepsilon_i$ (2)
$Y_i = \alpha X_i^{\beta} \varepsilon_i$ (3)
Y_i = total length of the fish in mm
X_i = length of scale in mm (caudo-dorsal radius)
ε_i = random variable

The body length was chosen as dependent variable, since the back-calculation of fish lengths is done from the scale. Model 1 is the equation of the straight line. Model 2 is a polynomial tested for X up to the fifth order. Stepwise multiple linear regression has been applied to this model. In model 3 the relation is considered exponential. It has, however, been transformed to linearity by using logarithms: $\ln Y_i = \ln\alpha + \beta \ln X_i + \ln\varepsilon_i$. The equations are presented in Table 1, and the length observations in Fig. 2.

In all equations except 3: 2 and 3: 3 the mean value of six scales from each fish has been used in the calculations. In 3: 2 and 3: 3 only one scale is included. As is evident from the table, equation 3: 1 has the highest R^2-value (for $R^2 = 1$ all observations lie on the predicted line). For model 3 the existence of an intercept not equal to zero has also been tested (FRY, 1943). This was done by trying different values of c in the equation $\ln(Y - c) = \beta \cdot \ln X + \ln\alpha$. An intercept of 1 mm (Fig. 3) gives the highest R^2. In view of the accuracy of measurement this intercept can be neglected.

Method of estimation

The best fit is achieved for the values of α and β, which give a minimum of $\Sigma\varepsilon_i^2$ ("least/squares method"). ε_i (the residuals) are assumed to be normally distributed (see Fig. 4 a—c), with the mean value zero and independent. Another condition, that of constant variance of ε_i, was tried by a test of BARTLETT described by BROWNLEE (1964: 290—95), see Table 2.

The test gives a significant result at the 1 % level for model 1, the straight line; this seems reasonable considering the data. For the exponential model (3: 1) BARTLETT's test gives a clearly non-significant result (Figs. 2, 4).

The lack of fit has been tested by an F-test given in DRAPER and SMITH (1966: 26—32). The result is shown in Table 3.

This test gives a significant result at the 0.01 level for model 1, *i.e.* the assumption of linearity is not appropriate for this model. Model 3 gives a better result in this respect.

The variability of the scales

As has been mentioned above the mean value of six scales from each fish was used in the calcula-

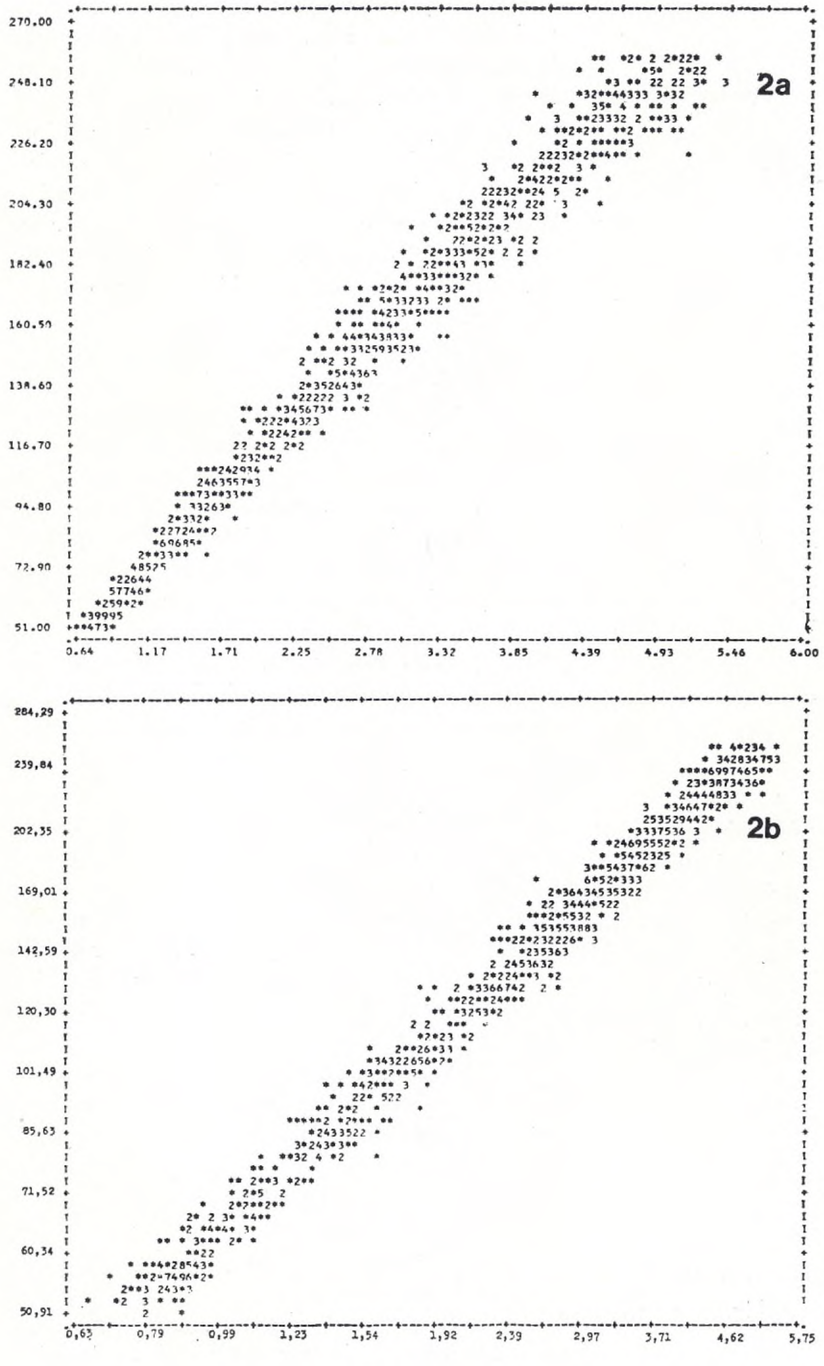


Fig. 2 a. Scattergram of body-length (mm) on scale-radius (mm).
Fig. 2 b. Scattergram of log body-length (mm) on log scale-radius (mm). *=one observation, 9=nine observations.

tion. The possibility that the variance of these mean values is affected by the size of the fish was investigated by forming the regression of this variance on the body length. The regression equation becomes Y=0.00082X+0.01612 (X being the body length) and $R^2=0.43$. The corresponding plot is shown in Fig. 5. As is evident from the equation and the plot, the correlation is positive

Table 1. *The regressions of fish length on scale radius with R^2-values (the square of the multiple correlation coefficient).*

Model number	The regressions with estimated parameters	R^2
1	$Y=23.09+45.75X$ (0.18)	0.9828
2:1	$Y=13.60+57.27X-0.231X^3$ (0.47) (0.016)	0.9857
2:2	$Y=18.68+47.35X+0.403X^3-0.096X^4$ (1.15) (0.136) (0.021)	0.9860
2:3	$Y=18.10+48.28X+0.052X^4-0.015X^5$ (0.70) (0.023) (0.004)	0.9860
3:1	$\ln Y=\ln 65.84+0.8244\cdot\ln X$ (0.0027)	0.9880
3:2	$\ln Y=\ln 66.40+0.8123\cdot\ln X$ (0.0036)	0.9795
3:3	$\ln Y=\ln 66.60+0.8169\cdot\ln X$ (0.0035)	0.9818

(The standard error of the parameters is given within brackets)

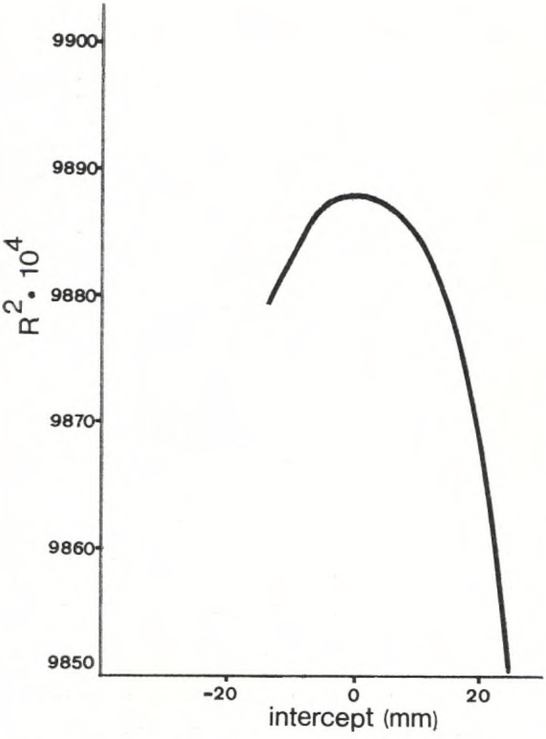


Fig. 3. The square of the multiple correlation coefficient as a function of the intercept (model 3).

Table 2. *Test of variance.*

Model number	Number of length classes	P-value
1	210	0.000
3:1	218	0.561

(The P-value is the level of significance. The null hypothesis is $\sigma_1^2=\sigma_2^2=\ldots=\sigma_n^2=\sigma^2$, where n is the number of length classes.)

Table 3. *Test for lack of fit.*

Model number	Observed F-value	P-value
1	1.566	0.000
3:1	1.272	0.010

but very weak. On the assumption that the residuals are normally distributed (Fig. 4) and independent, the regression is significant ($F(1, 1085)=821.25 > F_{.95}(1, 1085)$) *i.e.* the regression coefficient differs from zero. The weak correlation may be due to the difficulty of sampling the scales from the correct area on the small fishes.

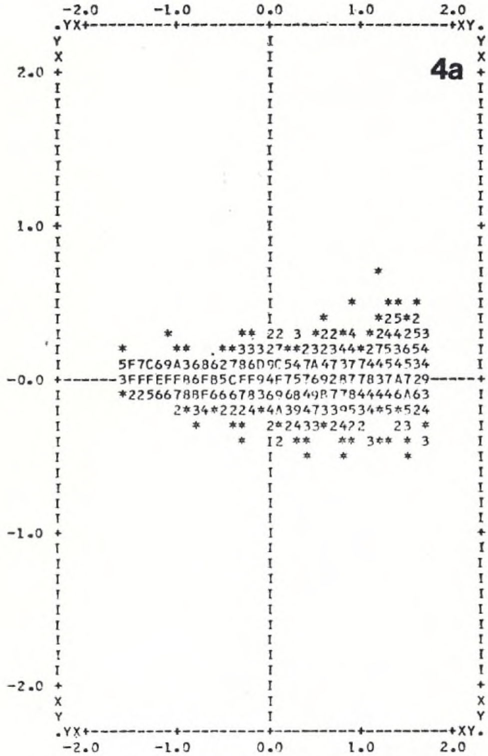
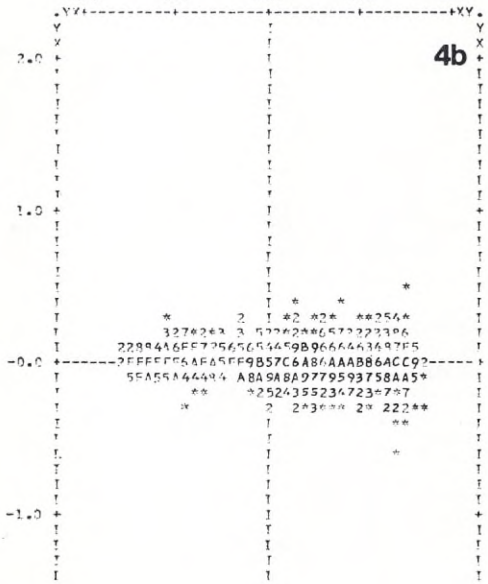


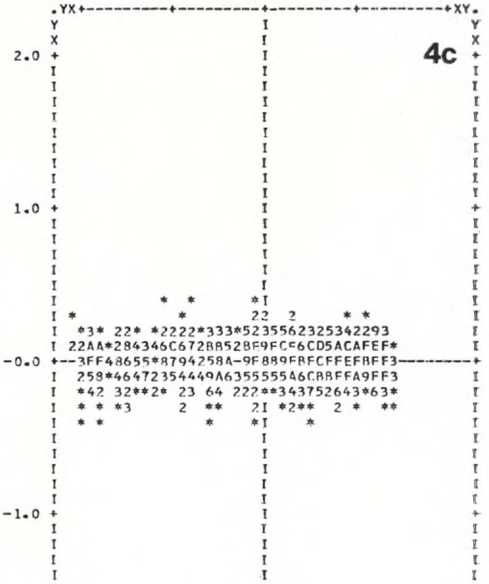
Fig. 4. Standardized residuals against standardized body-length.

Fig. 4 a. The straight line (model 1).

Fig. 4 b. The fifth degree polynomial (model 2).

Fig. 4 c. The logaritmic line (model 3).





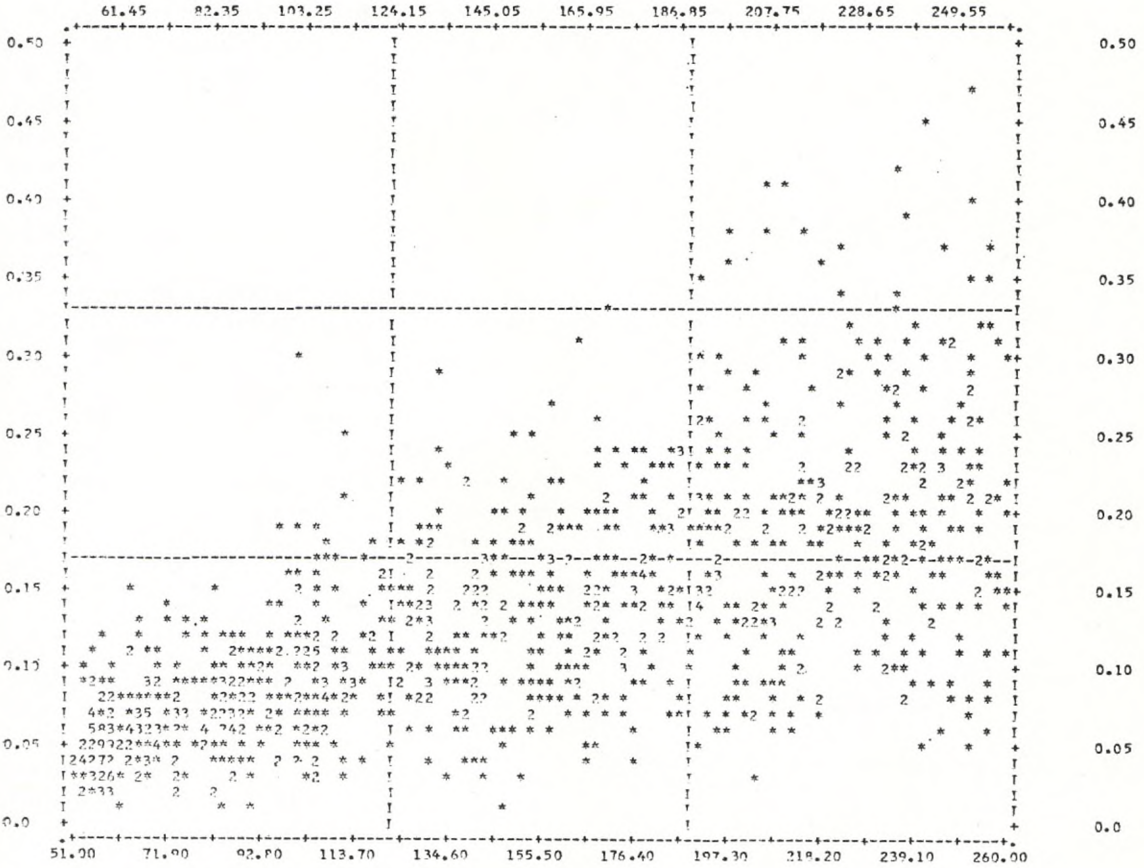


Fig. 5. Scattergram of the scale standard deviation on the body-length (mm).

Table 4. *Length of scale (mean values) for the "original" and the formalin-treated material for body lengths in the interval 50—63 mm. The differences are tested by "Students" (S) t-test and a treatment of this test by* WELCH (W).

Body length	"Original" material scale length (mm)	"Formalin" material scale length (mm)	t-value	Degrees of freedom	Critical t-value
52	0.848	0.856	0.20 (S)	4	2.78
54	0.831	0.856	5.01 (W)	3	3.18
55	0.800	0.944	4.33 (W)	2	4.30
57	0.871	0.986	9.41 (W)	16	2.12
58	0.870	1.088	9.30 (S)	21	2.08
59	0.880	1.001	2.08 (W)	4	2.78
60	0.941	1.036	2.95 (W)	4	2.78
63	0.957	1.113	3.71 (S)	5	2.57

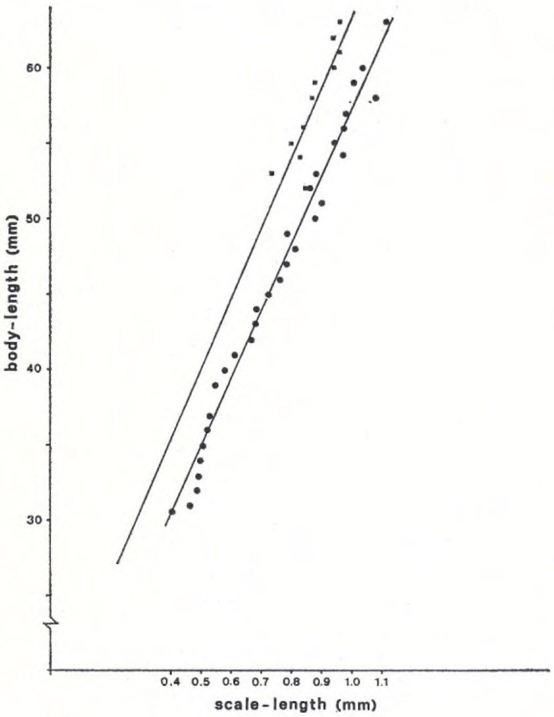


Fig. 6. Plot and regression lines of the "original" (■)- and the formalin-treated material (●).

The smallest fishes

As has been pointed out under "Material and methods" the material treated above does not include the length after the first year, normally 35—45 mm. To compensate for this deficiency, six scales from 130 formalin-fixed roaches 31—63 mm in length were measured. The mean scale radii for 1 mm body-length classes were compared with corresponding values from the main series (Fig. 6). The comparison was made by t-test (BROWNLEE: 1964. 297—303) for eight length classes within the interval 50—63 mm and gave significant differences at the 0.05 level for six of them, see Table 4.

The regression lines of the two samples were also compared with respect to parallelism (BROWNLEE: 1964. 349—351). The slope of the lines did not differ significantly ($t=0.34 < t_{.975}$ (16)). The regressions together with the one for 30—63 mm, are entered in Table 5.

As can be seen in the Table and in Fig. 6, the lines are nearly parallel and for the formalin-fixed material almost identical. Thus, the difference found by the t-test indicates that in formula 3:1 the constant (α) differs but the coefficient (β) does not.

IV. DISCUSSION

Among the tested models for the body/scale relationship the exponential one gives the best fitted regression. The polynomials gave somewhat better correlations than did the straight line. By varying the order of the polynom, introducing dummy variables, etc., it is likely that the residual variance will be smaller than for the exponential model. However, the correlation coefficient for this is so high that such manipulations would probably give an unnecessary complicated and less general model without biological significance.

It is difficult to make comparisons with earlier works on roach as different scales and radii have been measured. In the present investigation, the body area from which the scales were taken, and

Table 5. *Regression lines of the "original" and the formalin-treated material in the body-length intervals 50—63 mm and 30—63 mm.*

		R^2
"Original" material (50—63 mm):	$Y=16.52+46.95\cdot X$ (14.73)	0.8775
"Formalin" material (50—63 mm):	$Y=13.11+43.76\cdot X$ (9.99)	0.9880
,, ,, (31—63 mm):	$Y=13.39+43.55\cdot X$ (1.81)	0.9155

(The standard error of the parameters is given within brackets.)
Y=body length
X=scale length

the radius were chosen according to KEMPE (1962). That author found, however, that scales from area III (Fig. 1) have less variance than the ones here chosen (area IV). In Sweden, however, area IV has been generally used. KEMPE constructed a curve according to EINSELE (1942) describing the body scale relationship for roaches caught in Lake Mälaren 1957—59. Assuming an exponential form of this curve, the regression coefficient has been calculated for body lengths between 50 and 260 mm. The first three places of decimals coincide with the coefficient calculated from the material presented here (model 3:1). It has not been possible to test this fact statistically, as KEMPE's material has disappeared.

The small roaches cause special problems. According to ALM (1922), the scales are not formed until the roach has reached a length of about 20 mm. Still, the exponential equation has a negligible intercept, and the body scale relationship seems to be the same for fishes between 35 and 60 mm. Moreover, judging from the mean values plotted in Fig. 6, just below this interval the scales grow slower than the body. These observations indicate that the scales grow faster than the body in the period just after the formation, which is also shown by FRANK (1970). It seems futile to try to fit equations to these processes. The soundest and most practical way would seem to be to use the exponential model also for the growth of the first year, which seldom falls below 35 mm.

V. SUMMARY

The body scale relationship in roach from a Baltic archipelago was investigated for 1,100 females arranged in length groups with a class width of 20 mm extending from 40 mm to 260 mm (total lengths), 100 in each group. Six scales were measured from each fish. A sample of 130 small fishes, 30—63 mm, was studied separately.

A very good fit was achieved when introducing means of the six scales from each individual into the formula: $\ln Y = \ln 65.84 + 0.8244 \cdot \ln X$. On the basis of this equation body lengths may be back-calculated as follows: $L = L_s \left(\frac{r}{R}\right)^b$, where L = back-calculated body length, L_s = final length, r = intermediate scale radius, R = total scale radius and $b = 0.8244$.

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