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INSTITUTE OF FRESHWATER RESEARCH

DROTTNINGHOLM

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Contents

Feeding habits of a sculpin (*Cottus gobio* L. *Pisces*) population

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Contents

I. Introduction

While there is a rich literature on the food ecology of economically important species of fish there are few studies on the subject concerning coarse fish. Species of this group generally are dealt with from the point of view of food competition with species utilized by man and most often with emphasis on the latter.

In the widespread common sculpin (*Cottus gobio* L.) there is information available mainly from England, where the species was studied by SMYLY (1957) and its feeding relationships to trout (*Salmo trutta* L.) and salmon (*Salmo salar* L.) by CRISP (1963) and MANN and ORR (1969). In the closely related sculpin species *C. poecilopus* HECKEL STRAŠKRABA *et al.* (1966) discussed food relationships to trout and minnow (*Phoxinus phoxinus* L.).

The purpose of the present investigation was to study the feeding habits of a dense population of *C. gobio*. Emphasis was on intraspecific variation with regard to size and season. Also, comparison was made with the food of trout; the only other relatively abundant fish species.

55° 33´ N
13° 53´ E
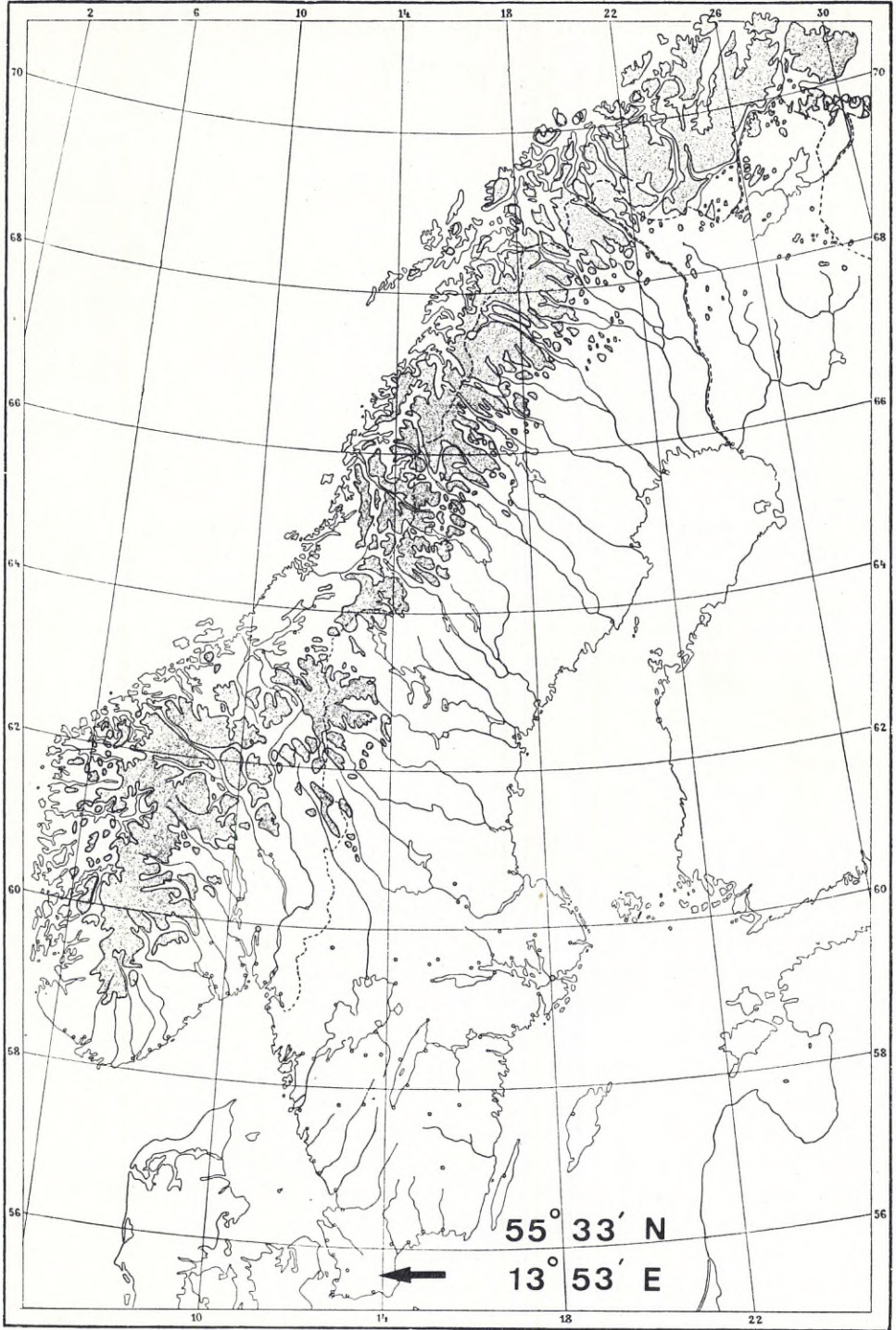
Fig. 1. Site of the investigation.

Table 1. Recorded variation of some physico-chemical parameters of the water of the stream Trydeå in 1964—65. Analysis was made on every fishing occasion (*cf.* Table 4).

pH	7.3—8.2
Specific conductivity ($\varkappa_{20} \cdot 10^6$)	530—630
Total hardness (DH°)	13— 22
Alkalinity mekv/l	1.8—4.0
Colour mg Pt/l	20— 40
O_2 %	74— 93

II. Description of the habitat

Trydeå ((55°33′N, 13°53′E; Fig. 1) is a swift-running eutrophic stream; a hard water or chalk stream in the British sense (Table 1). In the winter 1964—65 there was no ice-cover and thus sampling was possible throughout the year; lowest temperature recorded was 2°C (January 1965). Highest temperature during the investigation was 16.5°C (May and August 1964).

The investigation was carried out on a 150 metres' long portion of the stream at the village Ramsåsa. The average width of the stream is here 5.5 m and the depth 0.25—0.75 m, with an average discharge of 0.9 m³/sec. The bottom consists of medium sized to large stones alternating with smaller areas of gravel and sand. The stones have a cover of filamentous algae (*Cladophora* sp.) and moss (*Amblystegium* sp.). Along the stream banks there are scattered mud banks. The stream is sparsely bordered by trees and in summer there is a marginal dense macrophyte vegetation at places.

The fish community is dominated by sculpin. Trout of small size are, however, rather abundant. In the marginal mud banks ammocoetes larvae of the brook lamprey (*Lampetra planeri* BLOCH) are abundant locally. In less swift reaches three-spined stickleback (*Gasterosteus aculeatus* L.) are found. Occasional species are nine-spined stickleback (*Pungitius pungitius* L.), minnow (*Phoxinus phoxinus* L.), eel (*Anguilla anguilla* L.) and burbot (*Lota lota* L.).

III. Material and methods

A study of the feeding habits throughout a year of a population presupposes sampling of the same area on every occasion. As sculpin are stationary benthic fish the procedure of removing fish for preservation and later examination was abolished as it would change the population. The approach chosen included stomach pumping on live fish captured by electro-fishing. After treatment the fish was returned to the same part of the stream where it was previously caught. For stomach pumping an india-rubber bulb with a glass-tube inserted was used, *i.e.* a simplified Seaburg pump (SEABURG 1956).

Table 2. Size classes of sculpin and trout at stomach pumping.

Size class	Length cm		Size class	Length cm	Mean length cm
Sculpin:			*Trout:*		
1	1.2— 2.2		1	5.0—10.0	8.0
2	2.3— 3.7		2	> 10.0—20.0	15.0
3	3.8— 5.2		3	> 20.0—50.0	26.0
4	5.3— 6.7				
5	6.8— 8.2				
6	8.3— 9.7				
7	9.8—11.2				
8	11.3—12.7				

The efficiency of the stomach pumping was checked by dissecting some fish and was found to be adequate.

Sampling was carried out about once a month. Fishing was performed in the morning and specimens of sculpin and trout were treated. The following procedure was used:

1) Electro-fishing 1—2 hours.
2) Size classification 30 minutes.
3) Stomach pumping of the separate size classes 2—4 hours.
4) Fish returned to the water.

Small specimens of sculpin (< c. 3 cm) were not possible to treat by stomach pumping. A sample of 50 specimens of the first year class was preserved on every occasion from July 10, 1964, on.

Table 2 shows the size classes at stomach pumping (Arabic numerals). For most calculations the sculpin population was subdivided into three classes (Roman numerals) roughly representing the age groups 0, 1 and 2—4, respectively (Table 3). The distribution on the various size classes of the different samples is given in Table 4. The material comprised 2,110 sculpin and 308 trout. In addition 255 sculpin were sampled and preserved on Sept. 25 and Oct. 10, 1965 to get data on length, weight and age.

The identification of food organisms was carried out to the order level with some exceptions: as regards *Diptera* larvae the families *Chironomidae*, *Simuliidae* and *Tipulidae* were separated from other *Diptera* (mainly *Tabanidae*). Macroscopic *Crustacea* and fish were classified to species. Imagines of terrestrial insects occurred in trout only and were not subdivided any further.

The stomach contents of all individuals of each size class were treated as a unit. The number of food items of each food group of Insecta was accurately determined by counting chitinous head capsulae, or mandibles when only fragments remained. The mean weight of whole organisms found in the stomach content was determined for each size class (wet weight). This

Table 3. Size classes of sculpin used in most calculations (Roman numerals) and their correspondence to size classes at stomach pumping (Arabic numerals).

Size class		Length cm	Approximate weight g	Number of stomachs
Calc.	Pump.			
I	1—3	1.2— 5.2	0.02— 1.5	690
II	4—5	5.3— 8.2	1.5 — 5.5	871
III	6—8	8.3—12.7	5.5 —25.0	559

was done on the complete material disregarding variation between samples. The weight of the stomach contents was calculated by multiplying the number of food items with the mean weight for the separate food groups. The weights so obtained were considered to be more reliable than those actually measured which did not account for the differential rates of digestion of various food items. Preserved fish specimens were analysed individually as to stomach content and the values added to the appropriate size classes.

Length and weight values refer to specimens preserved in 75 % alcohol. Length is given as total length. Otoliths were preserved in alcohol, treated

Table 4. Investigated material of sculpin and trout.

Size class	1964											1965					S:a
	11/3	14/4	10/5	10/7	24/7	10/8	24/8	19/9	21/10	9/11	18/12	29/1	31/3	8/5	4/6	30/6	
C. gobio																	
1	—	—	—	5	—	—	—	—	—	—	—	—	—	—	—	58	63
2	5	—	—	35	50	29	19	5	—	3	3	5	5	—	—	—	159
3	—	50	33	—	—	20	30	45	44	47	50	38	52	39	20	—	468
4	16	20	64	37	18	15	13	16	21	43	23	28	19	47	74	—	454
5	16	17	23	33	14	22	23	19	14	73	30	36	20	32	45	—	417
6	5	3	14	18	28	33	32	25	19	63	21	15	21	28	28	—	353
7	11	27	13	5	—	1	5	5	5	38	7	24	15	7	13	—	176
8	1	—	—	2	1	—	1	—	—	—	2	—	6	3	4	—	20
1—8	54	117	147	135	111	120	123	115	103	267	136	146	138	156	184	58	2110

Size class	1964										S:a
	11/3	14/4	10/5	10/7	24/7	10/8	14/8	24/8	19/9	21/10	
S. trutta											
1	22	19	15	8	8	9	11	16	15	16	139
2	1	1	1	12	14	14	23	23	24	24	137
3	—	—	2	3	—	1	5	4	3	14	32
1—3	23	20	18	23	22	24	39	43	42	54	308

in xylol for one day, cemented in DPX and read in microscope in reflected and transmitted light.

Terminology is mainly according to RICKER (1968).

IV. Population structure

The sculpin population was very dense. Estimations by capture-recapture procedure indicated densities of 12 ind./m² in the spring and 25 ind./m² in the autumn (ANDREASSON 1969) (Table 5). From the length frequency of the captures (ANDREASSON *op. cit.*) and the length-weight relationship (Fig. 2) the biomass could be calculated at roughly 30 g/m² in the spring and 60 g/m² in the autumn. These figures correspond to a total weight of 17 kg and 33 kg, respectively, per 100 metres of stream.

The age distribution (Fig. 4) points at a high turn-over rate. Fish of age group 4 (and possibly older) were uncommon. The growth was rapid during the first two growth seasons (Fig. 3); the males growing faster than the females which was evident already at an age of four months. The males reached the same average length in their second year of life as the females in their third (Fig. 5). The largest fish were always males although some females reached almost the maximum length of the males (*cf.* Fig. 2).

The sculpins of Trydeå spawned in their second year of life (1+).

V. Food of *Cottus gobio*

The most important food item of the present sculpin population was *Chironomidae* larvae. Besides, *Trichoptera* larvae, *Gammarus pulex* and *Ephemeroptera* larvae composed the food base (Table 6). Fish were occasionally found in large specimens and also large terrestrial invertebrates (*Lepidoptera* larvae and *Oligochaeta*) as well as large benthic animals (*Tipulidae* larvae, *Neuroptera* larvae and *Hirudinea : Herpobdella* sp.).

Chironomids dominated greatly in number in all three size classes but in weight only in small fish (Fig. 6). There was a continuous decrease in the

Table 5. Estimates of population density and biomass of sculpin.

Season	Density ind/m²		Biomass g/m²
	Age group 0	Age group 1—4	
Autumn 1.10.1968	20	5	60
Spring 16.5.1969	10	2	30
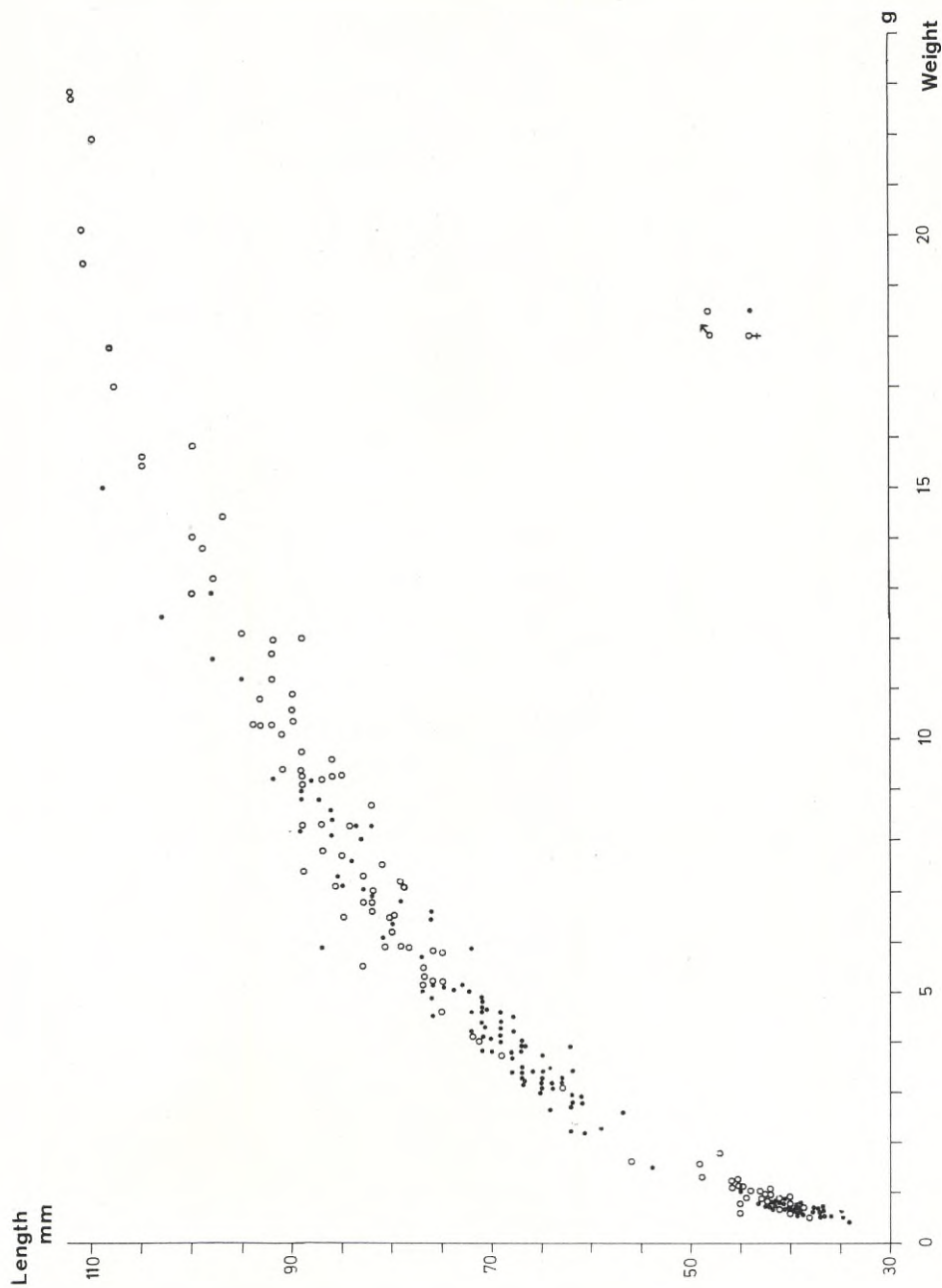
Fig. 2. Length-weight relation of *C. gobio* in samples 25.9 and 7.10.1965.
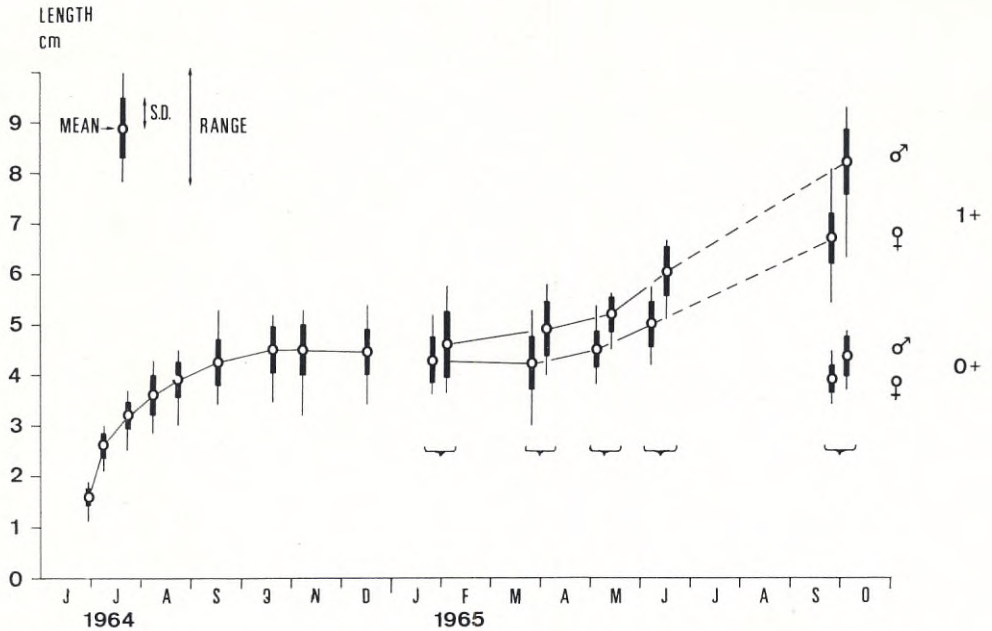
Fig. 3. Growth of *C. gobio* of age group 0—1. The first sample of alevins refers to the year 1965 but has been fitted to the series of 1964. Each sample comprises approx. 50 specimens. The last sample is identical with that shown in Fig. 4.

abundance of chironomids with increasing fish size (Fig. 7). Conversely, the number of *Trichoptera* larvae increased with fish size. In *Gammarus* and *Ephemeroptera* larvae there was no pronounced tendency in distribution according to fish size although the number of *Gammarus* was greatest in large sculpin.

The mean weight of the prey increased generally with fish size (Table 7). In the chironomids, however, this increase stopped at a fish length of about 6 cm while in *Trichoptera* there was a steady rise of the mean weight (Fig. 8); this as a result of the great difference in maximum size of the two food organisms. Thus the weight of *Trichoptera* will be pronounced in large sculpin (Fig. 6: III) and be of increasing importance with fish length when compared to the situation in chironomids (Fig. 9).

The average weight of food per individual increased greatly with fish size, whereas the average number of total food items per individual displayed a limited variation (Table 8). Actually there was a maximum number of food items per fish at a length of approx. 7.5 cm as a result of a predominance of *Chironomidae* larvae at this length (Fig. 10). The number of food items other than chironomids increased with fish size.

There was a slight seasonal variation in average number of food items per
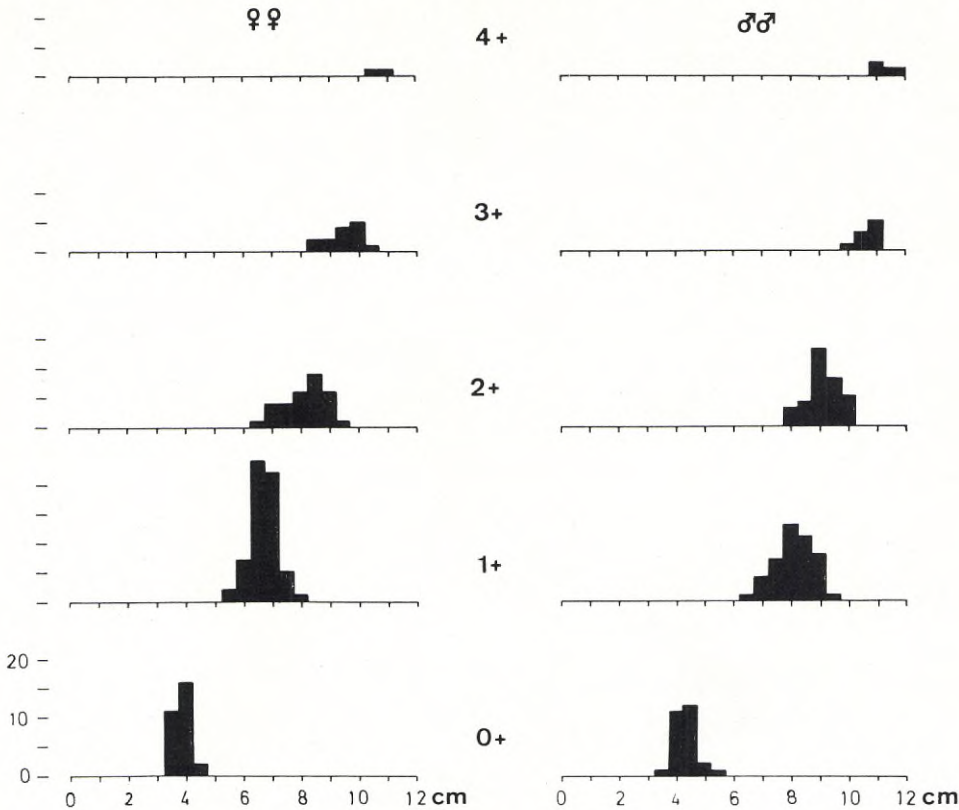
Fig. 4. Age distribution of *C. gobio* in samples 25.9 and 7.10.1965.

fish with a maximum in spring (Fig. 11). The same pattern occurred in all three size classes except a divergence in winter for size class I; the low number in winter was caused by low number of chironomids.

The seasonal variation in the number of *Chironomidae* larvae (Fig. 12) stresses the importance of this food group to small sculpin; chironomids generally made up 80—90 % except in the autumn. Large sculpin had on the whole lower values which varied strongly. In size class III a seasonal variation with a minimum in summer is indicated. With regard to the distribution on the various size classes of chironomids consumed by the population a marked seasonal variation appears evident (Fig. 13). For large sculpin food items other than chironomids were most important in spring and summer (Fig. 16).

VI. Food of *Salmo trutta*

The food base of small trout was similar to that of the sculpin population except for the terrestrial food items (Table 5, Fig. 14). In large trout fish
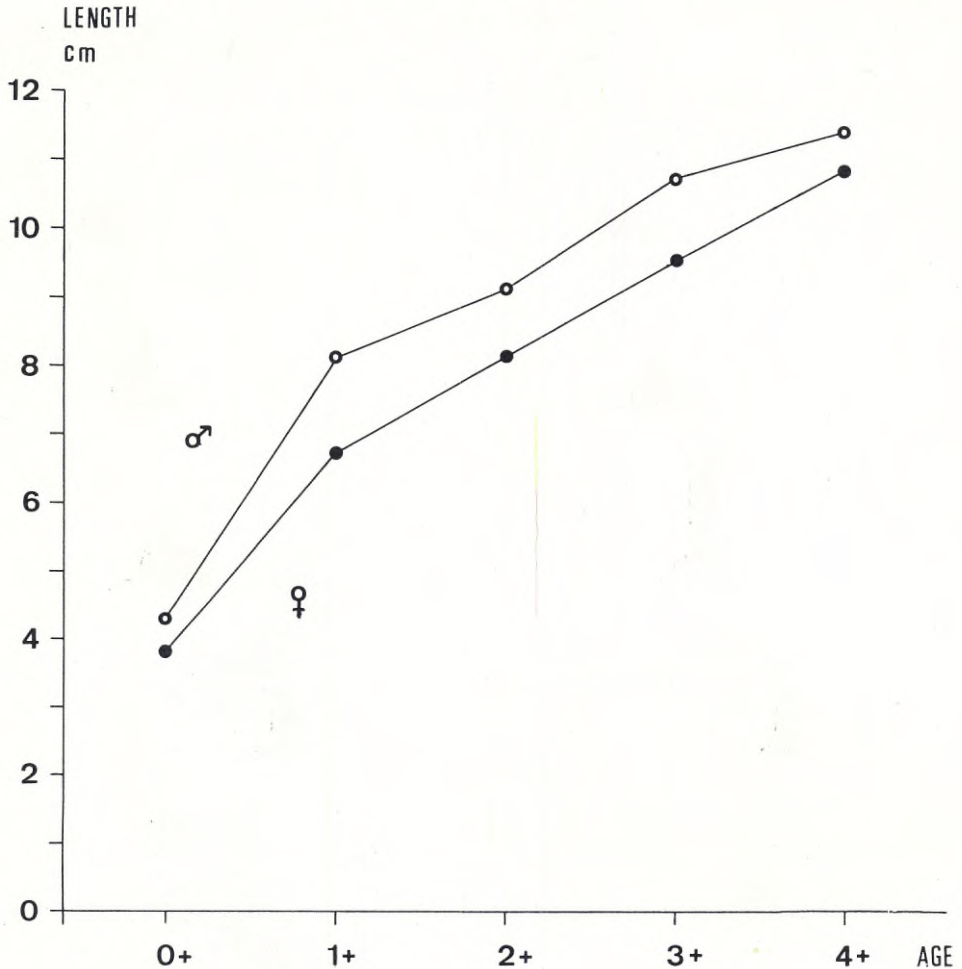
Fig. 5. Age-length relationships of *C. gobio* in samples 25.9 and 7.10.1965.

might be of importance (sculpin and stickleback). *Chironomidae* larvae were frequent only in small trout. Both sculpin and trout fitted a trend of decreasing dependence of *Chironomidae* (Fig. 15).

Gammarus was of greater importance in trout than in sculpin and dominated over *Trichoptera* larvae in large trout as well. In small trout *Ephemeroptera* larvae formed the bulk of food of aquatic origin besides chironomids. *Plecoptera* larvae were more common in trout than in sculpin and so were *Mollusca* (*Limnea* sp., *Ancylus* sp.); both groups occurring in greatest number in large trout. *Hirudinea* (*Herpobdella* sp.) constituted 11 % of the weight of food in trout of size class 2.

Table 6. Total number of food organisms found in stomachs of 2,110 sculpins
in 1964—65 (left) and of 308 trout in 1964 (right).

Trichoptera l.	2,572	413
Trichoptera p.	42	32
Ephemeroptera l.	990	656
Plecoptera l.	342	298
Neuroptera l.	37	—
Chironomidae l.	19,593	1,079
Chironomidae p.	1	203
Simulidae l.	186	129
Tipulidae l.	32	13
Other *Diptera* l.	234	26
Coleoptera l.	134	12
Coleoptera im. (*Helmidae*)	44	19
Hemiptera	2	14
Lepidoptera l.	4	13
Oligochaeta	17	6
Hirudinea	14	24
Mollusca	18	93
Araneida	8	42
Acari	2	11
Ostracoda	45	—
Copepoda	1	—
Asellus aquaticus	4	—
Gammarus pulex	1,357	606
Gasterosteus aculeatus	3	9
Pungitius pungitius	6	—
Cottus gobio	8	11
Roe of *Cottus gobio*	18	—
Terrestrial insects im.	—	1,020

The average weight of the prey increased with fish length with two
exceptions: in *Ephemeroptera* and *Plecoptera* the relation was the reversed
(Table 6). There was a great similarity in the weights of prey of small trout
and small sculpin where *Gammarus*, *Trichoptera* and *Chironomidae* larvae
are concerned. In *Ephemeroptera* larvae there was a close resemblance be-
tween small trout and large sculpin. Large *Trichoptera* larvae occurred in
trout of size class 3 and in large sculpin (size class 8 in Fig. 8).

The average number of food items per fish did not differ much between
the different size classes and was of the same order of magnitude as in large
sculpin (Table 7). The average weight of food per individual increased
rapidly with fish size as in the sculpin.

In spring when terrestrial insects were not available there was a close
resemblance in food composition between small trout and large sculpin
(Fig. 16). In summer and autumn a segregation as to the types of prey was
indicated caused mainly by the great number of terrestrial insects and
Chironomidae pupae in the food of trout. The trout showed a wider food
spectrum than the sculpin.

C.gobio
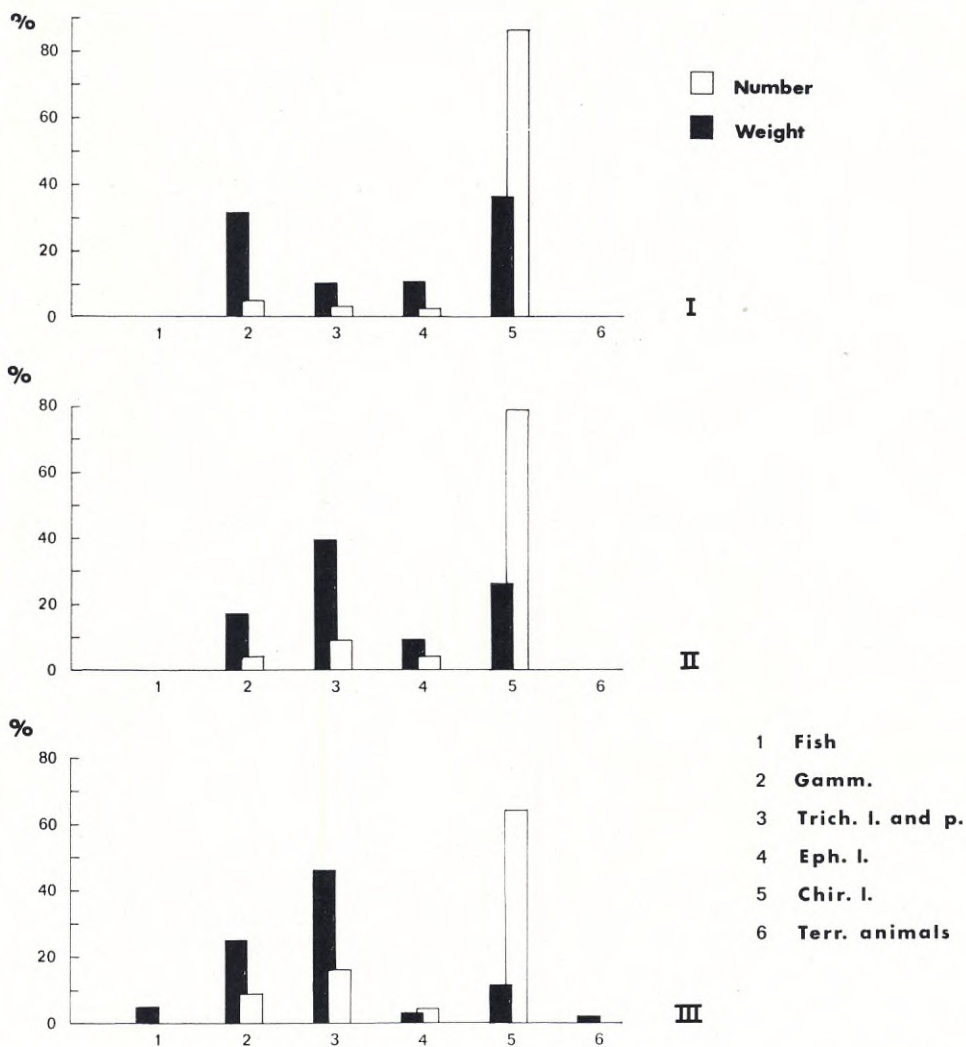
Fig. 6. Composition of food in *C. gobio* of different size. Only the most important food groups are considered (*cf*. Fig. 14).

VII. Discussion

Methods

The stomach contents of the individuals within each size class was not separated at sampling. To obtain the main features of the food ecology of the population it was considered of primary interest to compare different

C. gobio
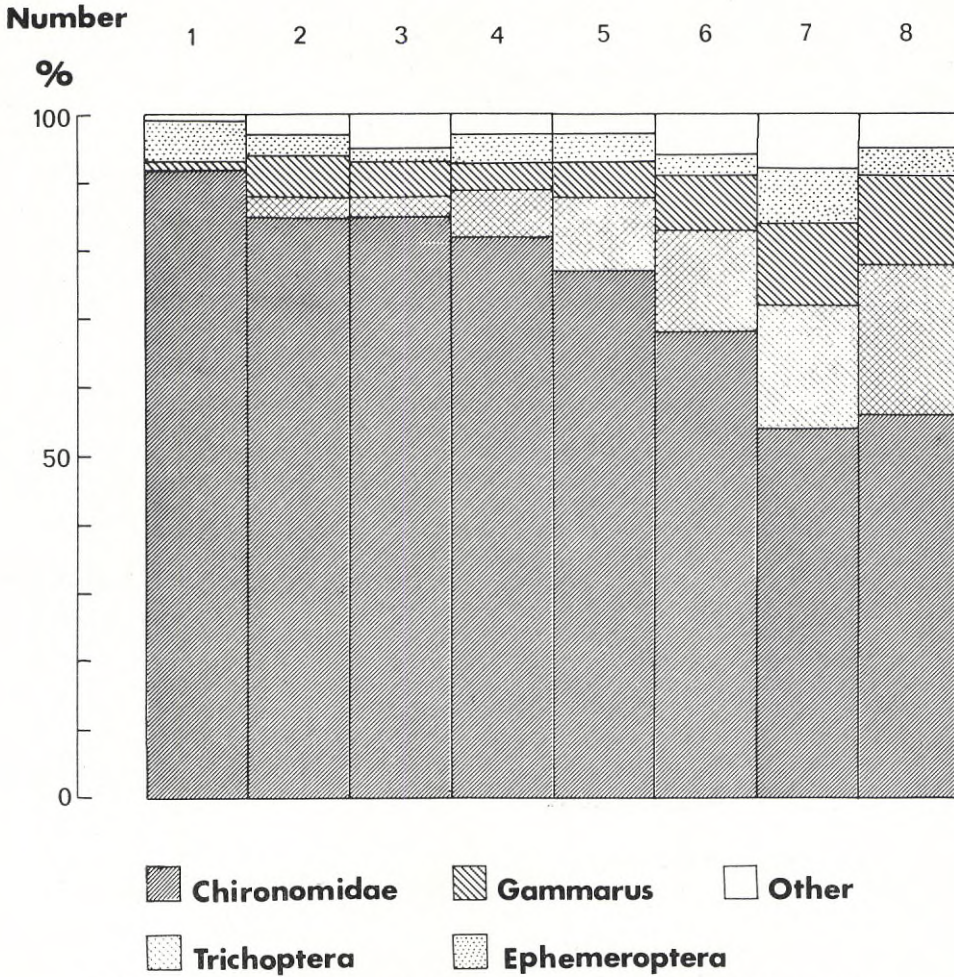
Fig. 7. Gradual change in composition of food in *C. gobio* of different size.

Table 7. Average weight of various food organisms of sculpin and trout (mg).

	C. gobio			S. trutta		
	I	II	III	1	2	3
Gammarus	3.1	12.3	19.8	6.1	21.1	18.6
Trichoptera l.	1.8	12.9	19.6	1.7	21.2	31.3
Ephemeroptera l.	1.9	6.9	4.9	5.6	4.4	4.2
Plecoptera l.	1.3	2.7	4.7	1.7	1.3	1.0
Chironomidae l.	0.3	1.0	1.3	0.2	(0.2)	—
Simulidae l.	—	—	1.6	1.7	1.9	—
Terr. insects im.	—	—	—	10.6	3.6	31.3

2

Prey animal

Average weight
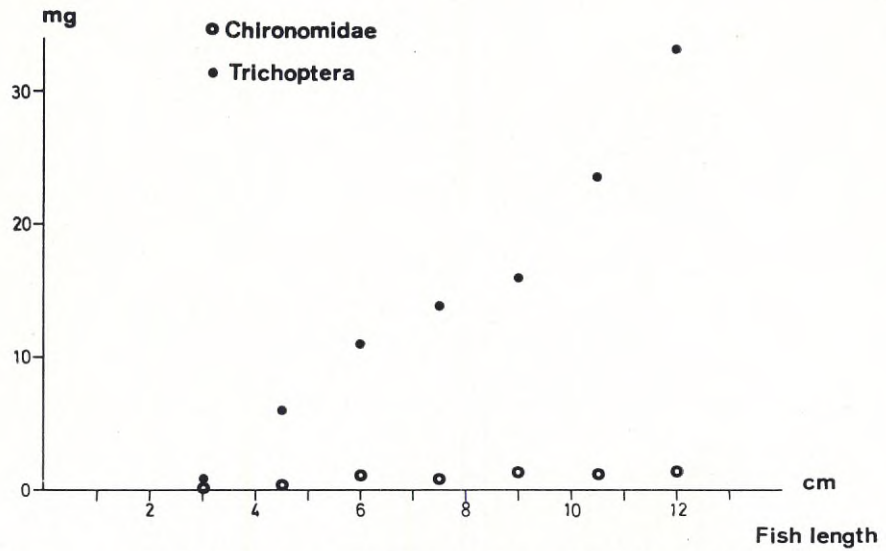
Fig. 8. Average weight of single larvae of *Chironomidae* and *Trichoptera* in the food of *C. gobio* of different size.

Relative

weight
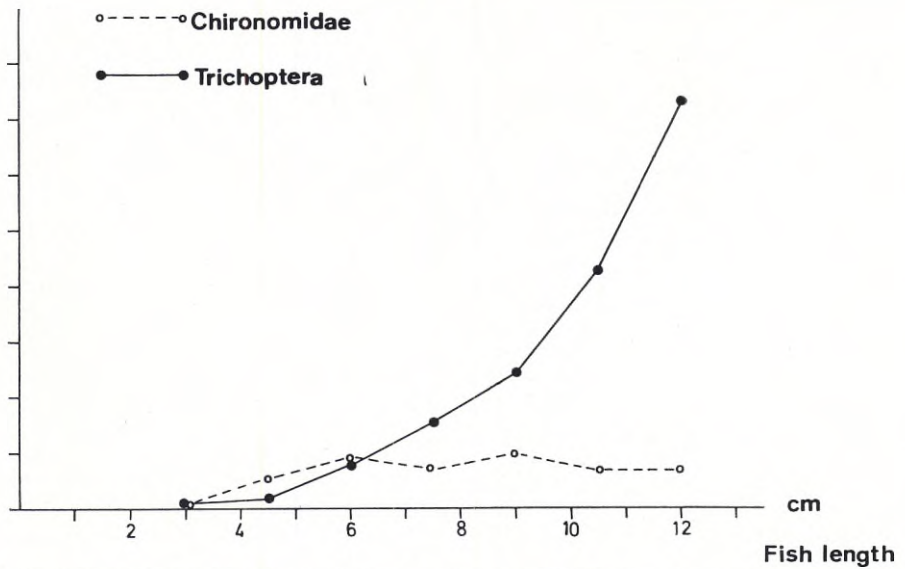
Fig. 9. Weight relationship between *Chironomidae* and *Trichoptera* larvae consumed by *C. gobio* of different size.

Table 8. Average number of food items and average weight of stomach content per individual of sculpin and trout.

	Number	Weight mg			Number	Weight mg
C. gobio				S. trutta		
I	7.8	3.7		1	13.6	38.3
II	14.2	43.9		2	16.9	159.9
III	14.7	109.2		3	16.6	535.3

size classes rather than individuals, why this simplified procedure was chosen. The disadvantages thus are that the number of empty stomachs and the individual variation in food composition are unknown. As both number and weight of the food organisms were determined the relative importance of each type of food could be evaluated. This material did not allow determination of mean weights of separate samples, *i.e.* the seasonal variation in average size of a certain food item eaten by sculpin of a certain size class could not be checked. Despite this approximation weight calculations based on the mean weights will give more accurate values than a direct estimation of the more or less digested stomach contents.
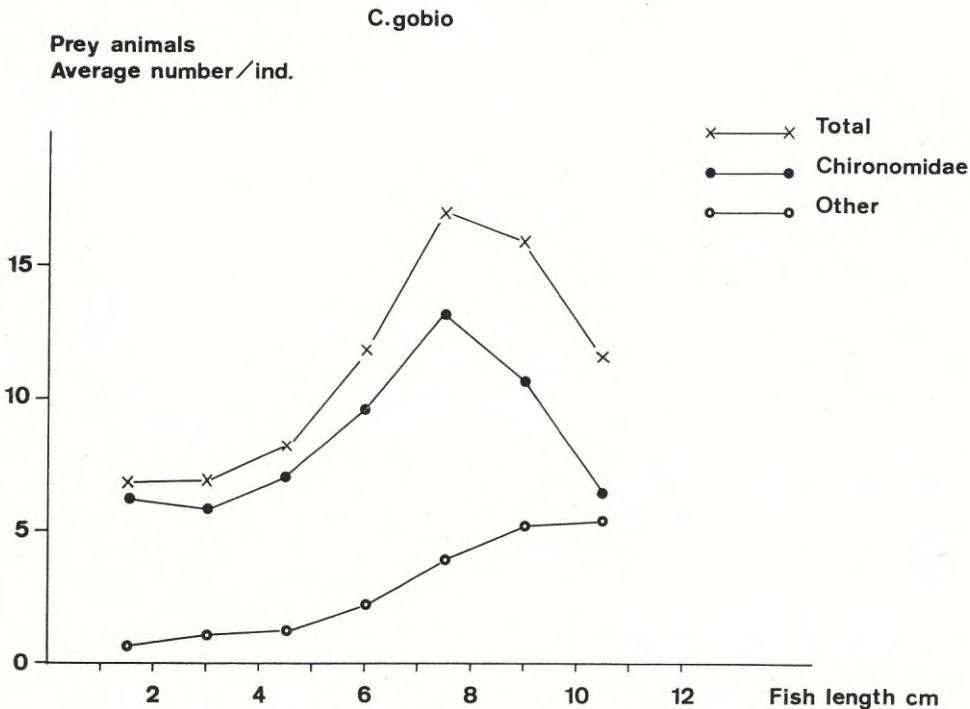
Fig. 10. Average number of food items per individual in *C. gobio* of different size. The number of *Chironomidae* larvae reaches a maximum at a fish length of approx. 7.5 cm while there is a continuous increase with fish length of other food items.

C.gobio

Prey animals
Average number ∕ ind.
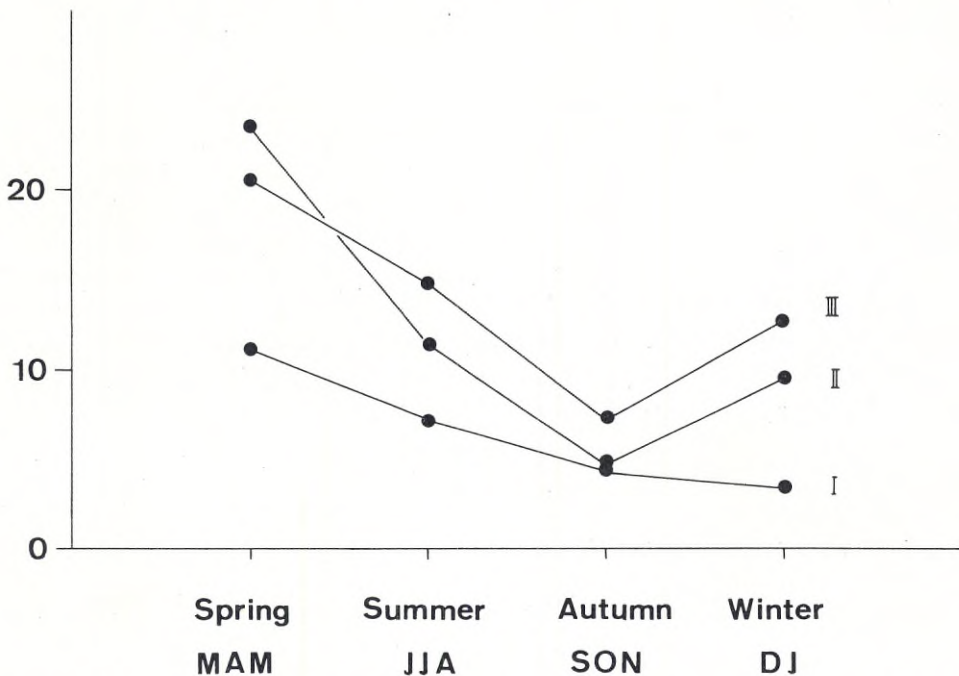
Fig. 11. Average number of food items per individual in *C. gobio* during the year.

As pointed out by SMYLY (1957) the age determination from otoliths is difficult in *C. gobio*. A structural difference was found between the otoliths of males and females, the latter having on the average more distinct annuli. The interpretation was therefore facilitated by reading the otoliths of each sex separately. Reflected light was used with the exception of large otoliths where transmitted light sometimes was found to be more useful. The annulus formation occurred in the spring.

Population density and growth

The density of sculpin in Trydeå was higher than hitherto reported in the literature. TUFFERY (1967) characterized *C. gobio* as very abundant and gave the value 5 ind./m²; the highest density recorded for the thirteen species investigated. MANN and ORR (1969) found a density of 13.5 ind./m² at one
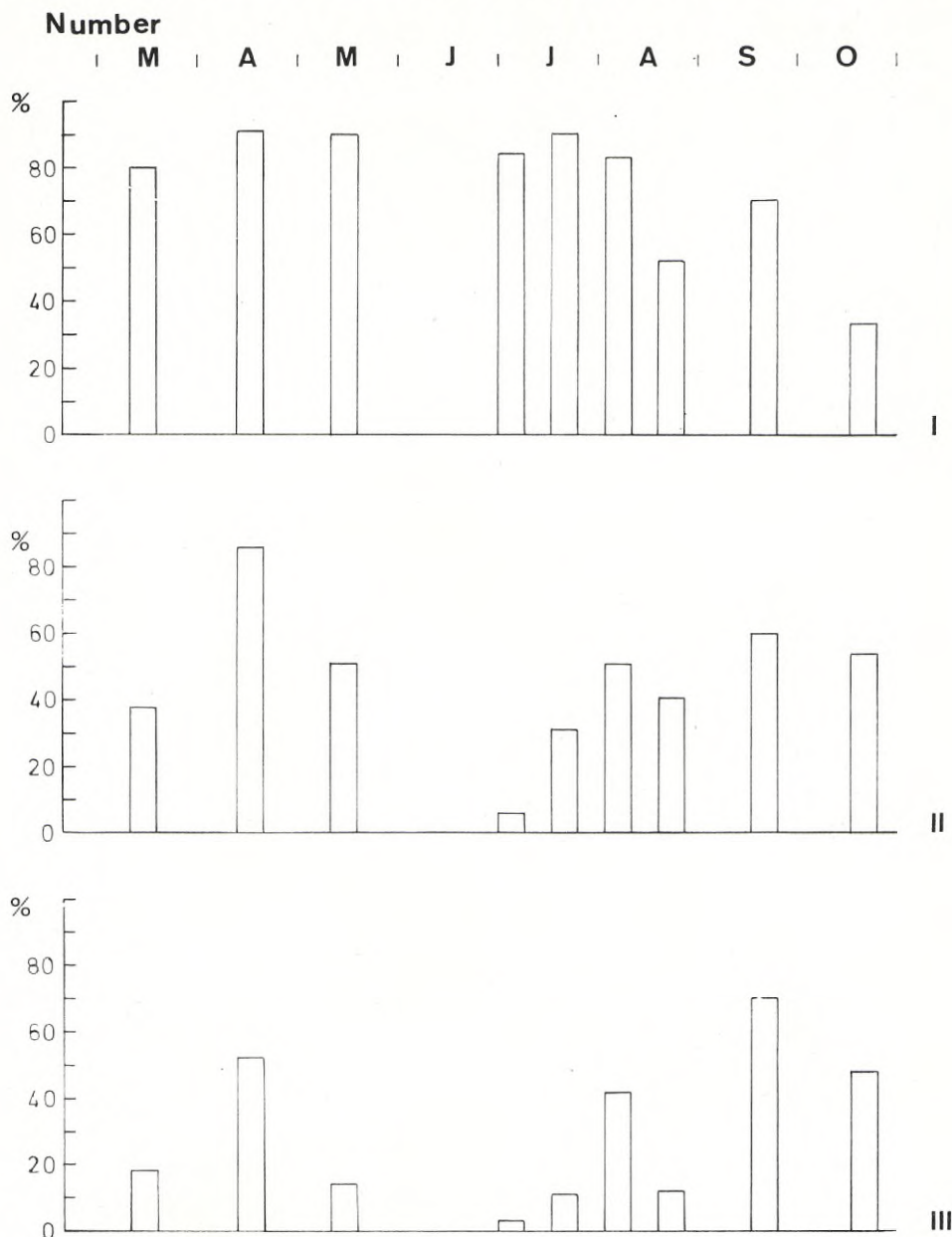
Fig. 12. Share of *Chironomidae* larvae during the year in the food of *C. gobio* of different size.

locality of Bere Stream (August); a hard water stream. A true comparison of density values is possible only if season and fish size are known. MANN (1967, 1971) presented a survival curve for *C. gobio* based on estimates of
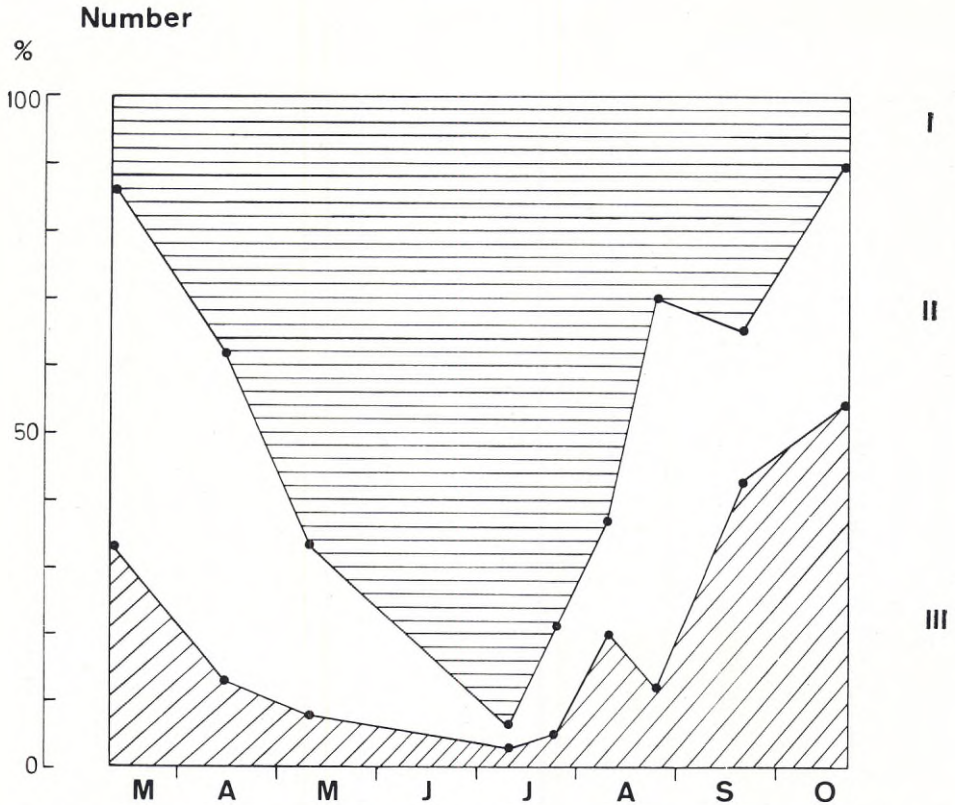
Fig. 13. Seasonal variation in distribution of *Chironomidae* larvae in different sizes of *C. gobio,* given as percental distribution of total number of larvae consumed by the population.

the density of the first and second year classes of sculpin every month of the year. The density of the first year class was in October determined at 10.3 ind./m². Estimates in Trydeå (ANDREASSON 1969) were made only on two occasions in the year (spring and autumn). The figures obtained fit the shape of the curve given by MANN (*op. cit.*) but point at a higher density throughout the year.[1]

The growth of *C. gobio* in Trydeå exceeds greatly the data given by SMYLY (1957), KÄNNÖ (1969) and MANN (1971). There is in general good agreement with the results of SMYLY (*op.cit.*) in the rapid growth during the first two seasons followed by a decline. KÄNNÖ (*op.cit.*) and MANN (1971) did not separate the sexes which makes a detailed comparison difficult as the males grow faster than the females.

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[1] By mistake values of number and biomass have been exchanged in MANN (1971: Table 21 and 22). Thus the high values 21.5 and 75.1 refer to biomass (g/m²).

S.trutta
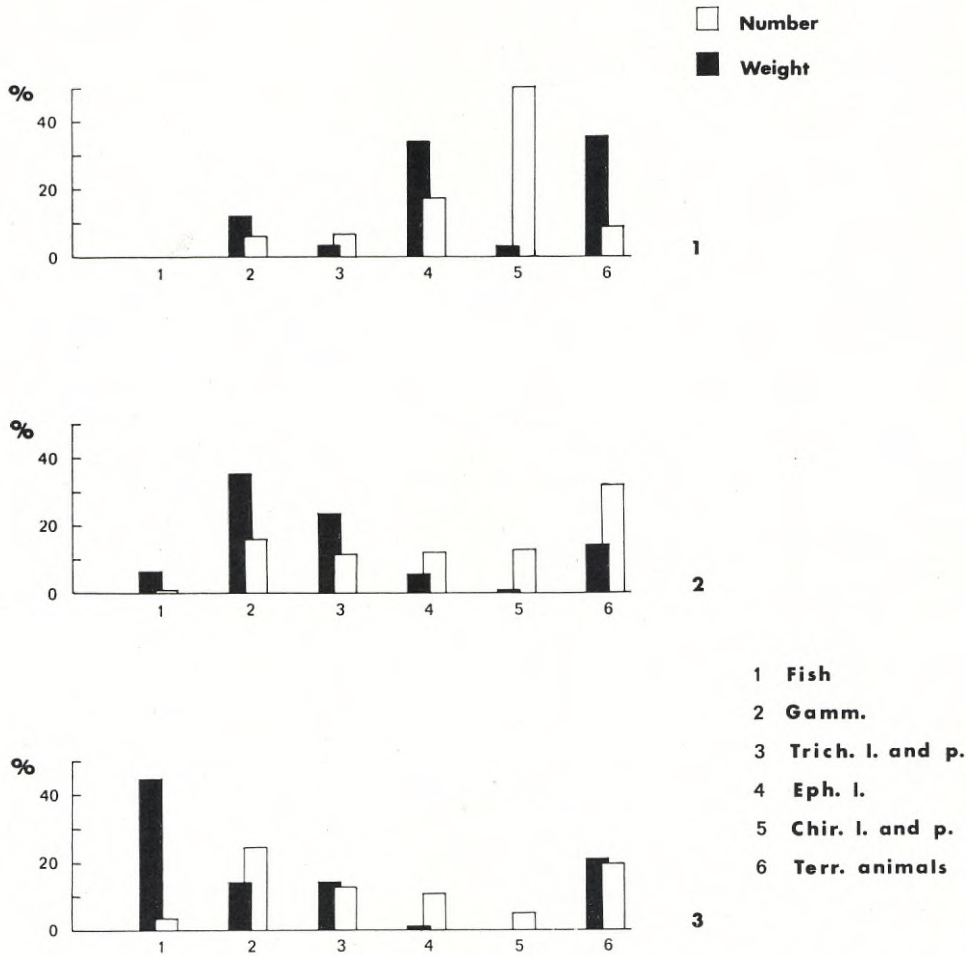
Fig. 14. Composition of food in *S. trutta* of different size. Only the most important food groups are considered (*cf*. Fig. 6).

The turnover rate in Trydeå seem to be similar to that of the populations studied by SMYLY (*op.cit.*); very few specimens live more than four years. The high turnover rate is also stressed by the results of MANN (1971).

Food range

The food base for the sculpin population in Trydeå is the same as that reported for the species in other investigations (CRISP 1963, HARTLEY 1948,

Chironomidae l. and p.
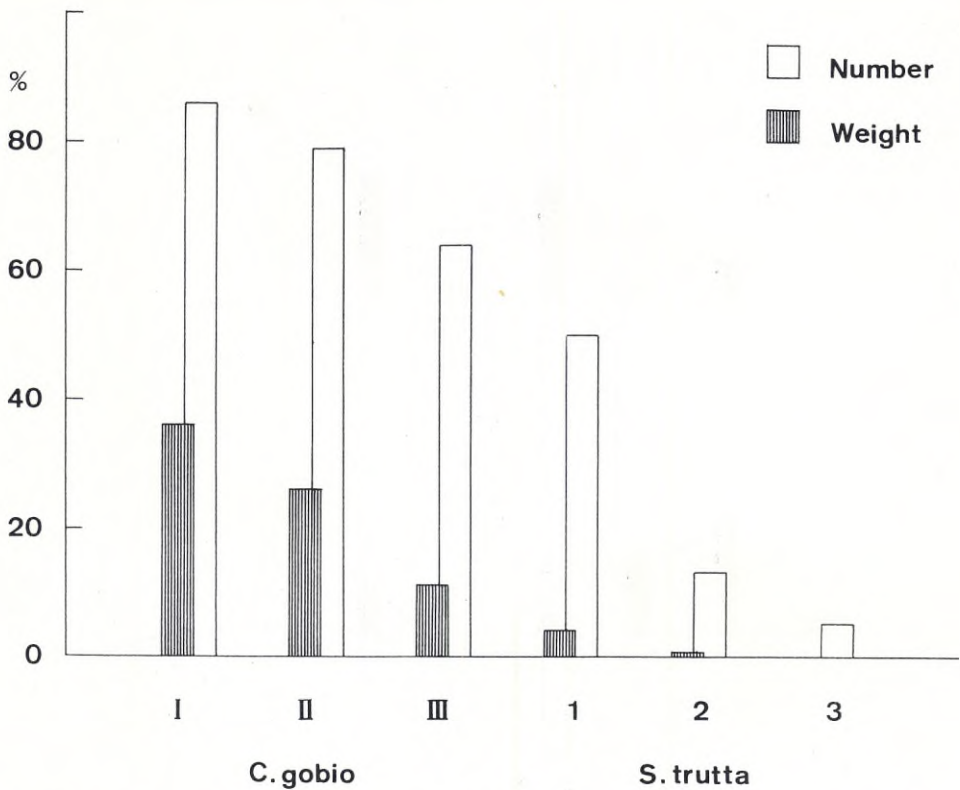
Fig. 15. The importance of *Chironomidae* larvae and pupae as food for *C. gobio* and *S. trutta* of different size.

MANN and ORR 1969, MÜLLER 1952, SMYLY 1957), *viz.* larvae of *Trichoptera, Ephemeroptera, Plecoptera, Diptera* : *Chironomidae* and *Crustacea* : *Gammarus* (when present). There is also a close similarity to the food of another European sculpin species, *C. poecilopus* (MÜLLER 1960, PASCHALSKI 1958, STRAŠKRABA *et al.* 1966) and of North American sculpin species, *e.g. C. bairdi* GIRARD (BAILEY 1952, DINEEN 1951, KOSTER 1937), *C. cognatus* RICHARDSON (KOSTER *op.cit.*) and *C. asper* RICHARDSON (NORTHCOTE 1954).

There are some differences in the importance of the separate food groups between the investigations cited but in general chironomids dominate in number. When different sizes of sculpin were examined this dominance of chironomids was pronounced in small specimens but the chironomids were successively replaced by larger food items with increasing fish length. In sculpin species with a maximum length of roughly 10 cm, like *C. gobio*, fish

S. TRUTTA   C. GOBIO
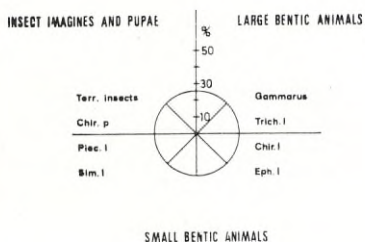
Fig. 16. Comparison in food composition during the year of small *S. trutta* and large *C. gobio*. In spring the same food groups were exploited by the two species, in summer and autumn there was a segregation.

is rarely a basic component of the food but was so in lake living *C. rhotheus* Rosa Smith and to a higher degree than in the cohabiting *C. asper* of the same length; 70—87 mm (Northcote 1954). The large Japanese sculpin *C. kazika* (Mizuno *et al.* 1958) feeds exclusively on fish at a length > 10 cm, but, when smaller utilizes a diet of the insect groups discussed.

Compared with the results of other investigations larvae of *Chironomidae* play a more important role in Trydeå. The very high proportion of chironomids found in the food of these sculpin may reflect a higher abundance of this particular food group than in other streams which have been subject to studies on sculpin food. Another possible explanation of the high values may be methodical: in the present study every head capsulum of *Chironomidae* larvae (even the smallest) was counted as one individual.

The seasonal variation of the amount of food consumed may hardly be evaluated from the amount of food found in the stomachs (Fig. 11) as the metabolic rate differs with season. What can be concluded is that sculpin are feeding throughout the year. This is in agreement with other investigations cited above and the same was true for the Baltic population of the fourhorn sculpin (*Myoxocephalus quadricornis* L.) (Westin 1970).

Intraspecific variation

Since the sampling was restricted to the same limited stretch of stream it was possible to analyse the annual variation in food composition within the population. The length of the fish was used as the base for subdividing the population. The qualitative composition of the food was the same in the different size classes of *C. gobio*, but various food groups were represented in different proportions (Figs. 6 and 7). There was a continuous replacement of *Chironomidae* larvae by other food items with increasing fish length (Fig. 10). This general pattern was found also in the North American sculpin *C. bairdi* by Bailey (1952).

The diminishing importance of chironomids and increase of other large benthic animals should be interpreted as an effect of size selection by the fish. It was shown to be an increase with fish length of the mean weight of most groups of prey (Table 6). The fact that the selective mechanism involved is highly sensitive is illustrated in *Trichoptera* and *Chironomidae* larvae (Fig. 8). The seasonal variation in distribution of chironomids on different size classes (Fig. 13) may also be interpreted as a result of size selection, assuming the food reflects the abundance of different sizes of prey, *i.e.* the high abundance of small *Chironomidae* larvae in late spring and early summer. This is in agreement with the low number of total food items found in the small sculpin during the winter (Fig. 11) since chironomids were the dominating food item this period as well.

In fish feeding on zooplankton a good correlation between size of prey

and predator has been found (BROOKS *et al.* 1965, GALBRAITH 1967). NORTH-COTE (1954) could explain differences in food size between two sculpin species as a difference in mouth width.

The average number of chironomids per sculpin reached a maximum at a fish length of approx. 7.5 cm. This small prey is thus, however abundant, not economical to large fish from the energy point of view (*cf.* Fig. 9).

Food relationships to trout

A close resemblance in food composition would be expected between small trout and large sculpin. This was also the case in spring with regard to the number of specimen (Fig. 16). As remarked above (p. 15) there was, however, in general a greater similarity in the mean weights of food items between small trout and small sculpin. Thus there may be a segregation as to food size although this cannot be positively proved as the mean weights of the different seasons are unknown. Since classification of the food items was not made to species there is a possibility of a segregation on different species as found by STRAŠKRABA *et al.* (1966) for the sculpin *C. poecilopus,* trout and minnow.

The general similarity of major food items of trout and various sculpin species in streams has been frequently reported (CRISP 1963, DINEEN 1951, KOSTER 1937, MANN and ORR 1969, MÜLLER 1952, STRAŠKRABA *et al.* 1966). The conclusions drawn from this overlap in food habits vary. HARTLEY (1948) pointed out that "between no two species is there a true identity of feeding habit" but "there is a great degree of general competition between all the fish of the community". STRAŠKRABA *et al.* (*op.cit.*) state that "there was little evidence of competition for food among the species" based upon the segregation on different prey species within the main food groups.

Some confusion in the interpretation wether or not competition for food exists seems to be derived from a difference in the conception of the criteria for competition: resemblance or divergence in food composition? As NILSSON (1960, 1963) has shown it may be both, or more precisely: the criterion is divergence — interactive segregation (NILSSON 1967) — if, under certain conditions, a close resemblance may occur (*e.g.* by superabundance of food or when the species are separated). Thus identity in food composition means that under prevailing conditions no severe competition exists.

The similarity of food of sculpin and trout in spring (Fig. 16) may reflect a situation of no severe competition, but, may also indicate that a competitive situation between the species can develop. The summer and autumn situation, on the other hand, may illustrate that competition is diminished by interactive segregation.

BROCKSEN *et al.* (1968) studied the problem of competition for food between trout and the sculpin *C. perplexus* in laboratory streams with simpli-

fied communities containing only two sorts of prey (*Chironomidae* and *Plecoptera* larvae). They found that "there seem to exist differences in the nature of the competition between these species. The sculpins compete directly with each other and can influence the food consumption and production of the trout through cropping the benthic food organisms directly, thus reducing the numbers of drifting organisms. The trout, on the other hand, affect the production of the sculpins very little because their consumption of drifting organisms does not usually materially reduce the benthic population of food organisms in the laboratory streams". The authors stress that the results from these experiments do not necessarily mean that such a competitive situation will appear under natural conditions. Their investigation, however, stresses the probability of an interaction between trout and sculpin also in nature.

VIII. Summary

The food habits within a dense population of the sculpin *Cottus gobio* L. were studied in a South Swedish eutrophic stream. Population density as well as growth was greater than earlier reported. Disregarding sculpin, trout was the only other abundant fish species. The food composition of the two species was compared.

1. The food composition of *C. gobio* was similar to that described for other small freshwater sculpins; the food base was benthic larvae of *Trichoptera, Ephemeroptera, Diptera* : *Chironomidae* and *Crustacea* : *Gammarus*. *Chironomidae* constituted the most important food item for the sculpin population.
2. There was a marked size selectivity of food items in relation to fish length. This appeared as a gradual replacement of *Chironomidae* larvae by larger food items, mainly *Trichoptera* larvae, with increasing fish length. There was also a positive correlation between the mean weight of the separate food organisms and fish length.
3. The exploitation of *Chironomidae* larvae as source of food reached a maximum at a sculpin length of approx. 7.5 cm.
4. There was a close resemblance in the food of sculpin and small trout during the spring but a segregation in the summer and the autumn. The probability of food competition between trout and sculpin is discussed.

IX. Acknowledgements

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Size and age at maturity, ripening and fecundity of the ide *Idus idus* (L.)[1]

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Contents

I. Introduction

Little attention has been directed towards maturity and fecundity of ide, *Idus idus* (L.) (OTTERSTRØM 1930—31, BERG 1949, POPESCU *et al.* 1958 and 1960 and BALON 1962). This study is based on ide collected in the River Kävlingeån, South Sweden, from November 1964 until April 1967, in the stretch Högsmölla to the mouth. The fishes were collected mostly by means of seine, bow-nets, weire-netting, and electro-fishing devices used by commercial fishermen in the water course. For further information see CALA (1970 a, b).

II. Size and age at maturity

An examination was made of 280 ide from the lower part of River Kävlingeån during the winters of 1966 and 1967. Fish with welldeveloped gonads apparently capable of producing gametes during the current year were con-

Table 1. Relationship of length to maturity in the various age groups of ide from
(All fish younger than the age group VI were

Total length intervals in mm	I		II		III		IV		V		VI		VII		VIII		IX		X		XI		Total	
	J	M	J	M	J	M	J	M	J	M	J	M	J	M	J	M	J	M	J	M	J	M	J	M
109—128	1	—																					1	—
129—148	1	—	1	—																			2	—
149—168					1	—																	1	—
169—188					6	—																	6	—
189—208					8	—																	8	—
209—228					4	—	1	—															5	—
229—248					4	—																	4	—
249—268					1	—	2	—															3	—
269—288							5	—															5	—
289—308					1	—	7	—															8	—
309—328							4	—	2	—													6	—
329—348							1	—	1	—	1	—											3	—
349—368									2	—													2	—
369—388									2	—													2	—
389—408											1	2											1	2
409—428													1	—	1	—			1	—			—	3
429—448											3	—	5	—	1	—	2	—	1	—			—	12
449—468													4	—	12	—	1	—					—	17
469—488													4	—	13	—	6	—	2	—	1	—	—	26
489—508													1	—			3	—	2	—			—	6
509—528																	2	—					—	2
529—548																					1	—	—	1
Total	2	—	1	—	25	—	20	—	7	—	2	5	15	—	27	—	14	—	6	—	2		57	69
Percentage mature	—	—	—	—	—	—	—	—	—	—	71	—	100	—	100	—	100	—	100	—	—	—	—	—

sidered to be mature. Sex was not determined for yearling and younger fish.
All ide shorter than 31.5 cm in total length were immature, and all longer
than 43.1 cm were mature (Table 1). The shortest mature male was 39.2 cm
long. All males were mature at lengths greater than 40.1 cm.

The first mature females appeared at 30.9—32.8 cm (shortest mature
individual measured 31.5 cm, except one at about 30 cm with the tail bent).
All females longer than 43.1 cm were mature. The smallest mature female
was 7.7 cm shorter than the smallest mature male but males reached 100 per
cent maturity at a length 3 cm less than the females.

All ide younger than age group VI were immature and all older than the
VII age group were mature. All males older than age group VI were mature
(*vide* Table 1).

According to OTTERSTRØM (1930—31) the male ides in Lake Arresø (Den-
mark) reach maturity earlier (in the 5th year of life) than the females (in
the 6th year). BERG (1949) reports that ide mature in the delta of the Volga
in their third year and in the River Kama in the 4th or 5th year. POPESCU

River Kävlingeån, in 1966 and 1967 (J=juvenile, immature, M=mature fish). immature and all older than group VII were mature).

Number of mature females in age groups

Total length intervals in mm	II J	II M	III J	III M	IV J	IV M	V J	V M	VI J	VI M	VII J	VII M	VIII J	VIII M	IX J	IX M	X J	X M	XI J	XI M	Total J	Total M
109—128	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
129—148	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—
149—168	—	—	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—
169—188	—	—	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	—
189—208	1	—	9	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	—
209—228	—	—	3	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	—
229—248	—	—	2	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—
249—268	—	—	1	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—
269—288	—	—	—	—	6	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	6	1
289—308	—	—	—	—	5	—	2	—	—	—	—	1	—	—	—	—	—	—	—	—	7	1
309—328	—	—	—	—	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—
329—348	—	—	—	—	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—
349—368	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	2	—
369—388	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	—	—	—	—	—	2
389—408	—	—	—	—	—	—	—	—	—	1	1	3	—	—	—	—	1	—	—	—	1	5
409—428	—	—	—	—	—	—	—	—	—	1	—	6	—	7	—	5	—	2	—	—	1	21
429—448	—	—	—	—	—	—	—	—	—	1	—	1	—	11	—	6	—	3	—	2	—	24
449—468	—	—	—	—	—	—	—	—	—	1	—	—	—	7	—	5	—	7	—	4	—	24
469—488	—	—	—	—	—	—	—	—	—	—	—	1	—	4	—	1	—	5	—	1	—	12
489—508	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1
Total	2	—	30	—	24	—	5	—	1	5	1	12	—	31	—	17	—	18	—	8	63	91
Percentage mature	—	—	—	—	—	—	—	—	83	—	92	—	100	—	100	—	100	—	100	—	—	—

et al. (1960) stated that in the lower part of River Danube the ide become mature at an age of 4—5 years and at a mean length of 26.5 cm and 32 cm, and at a weight of 200 g and 390 g respectively. Finally, BALON (1962) concluded that some ide specimens of Danube River, males and females, spawn in the second year, although the majority spawn in the 3rd and 4th years. A few immature female specimens were found in age groups V and VI. Of 149 ide examined by Balon and representing age group I throughout VI, all males older than age group IV were mature but this was not the case among the females older than age group V.

III. Ripening and fecundity

This study is based on ide collected in the River Kävlingeån at three-week intervals from November 1964 to May 1965 and every two months from April 1966 until April 1967. Total length, age (for 1966—67), and weight of the fish and their ovaries were recorded from the fresh material.

3

Ripening vs. egg size

Ripening females (2 weeks before the spawning) contained eggs in three stages of development: 1) Unripe: 100—500 μm diameter, clear, nucleated egg cells (100—300 μm diameter); and eggs with oil globule vaguely discernible — specially in the largest ova — with clouded appearence (300—500 μm diameter). 2) Ripening: 0.5—1.3 mm diameter. 3) Ripe: 1.30—1.85 mm diameter, mean 1.5. The eggs ready to be laid and fertilized have a diameter ranging between 1.4—2.1 mm, mean 1.7 mm. 24 hours after the eggs have been deposited they have a mean diameter of about 2.3 mm (range: 2.2—2.5 mm) (Table 2 and Fig. 1). Any apparent decrease in diameter of ova in stages 1 and 2 is aberrant. Eggs were examined in fresh condition as soon as possible after collection. Ripening females were distinguished from immature females at various seasons on the basis of egg size.

Quantitative analysis was made as follows. Since a similar distribution of egg sizes occurs in both ovaries of a female ide a combined random sample of eggs from the two ovaries was considered representative of the ovarian mass. The ovaries were slit and the eggs spread in tap water. Samples of loose eggs were placed on a lined diapositive photographic paper, and submerged in the water to keep their spherical form, and measured along two perpendicular axis to the nearest 0.1 mm. According to HIGHAM and NICHOL-SON (1964, cited by WYDOSKI and COOPER 1966) the method of averanging two measurements of each egg was shown to produce less variance in the samples than did the practice of using one measurement.

The diapositive was obtained from a photography taken of millimetre paper reduced 10 times so that, one centimetre on the millimetre paper corresponded to one mm on the negative (Dr. BERTIL ÅKESSON, pers. comm.).

The error associated with measuring eggs submerged in tap water was determined as follows. The diameter of one ripe egg was measured sequentially 30 times (i.e. the time required to measure 30 eggs from one female) while the egg was kept in the water and moved before each measurement (Fig. 2). The variation is distributed about a mean with no obvious trend: mean diameter 1.748 ± 0.0321.

Females that would be ripe in April can be distinguished from immature females as early as in the previous July on the basis of examining the mean diameter of 30 of the ova of the largest group (Table 2 and Fig. 1). It seems that older (or larger) fish ripen earlier in the season than do the smaller, which spawn for the first time, but the trend is unclear.

The ripening ova increase rapidly in size in June and early July. At this time the ova of the larger mature fish can be distinguished with certainty from the smaller by the ripening eggs. The largest increase in diameter of the ova occurs in August. The eggs have reached a mean diameter of about 1.30 mm in the middle of the month. In November the ova have the size

Table 2. Size of ripening and ripe eggs, and ripening index of the ide from River Kävlingeån. The means are based on measurements of 30 large ova from each female. * = ripe female or ready to shed its eggs.

Date	Total length of ♀♀ in cm	Mean diameter of eggs in mm	Ripening index	Date	Total length of ♀♀ in cm	Mean diameter of eggs in mm	Ripening index
1964				*1966*			
2.XI	43	1.40	11.44	20.VII	47	0.83	3.41
27.XI	48	1.52	17.65	"	49	0.84	2.90
"	48	1.47	18.37	"	41	0.83	3.75
"	48	1.61	17.60	11.IX	48	1.37	9.62
"	46	1.49	16.01	"	44	1.23	9.48
"	43	1.38	12.24	"	48	1.36	12.90
"	47	1.43	15.38	"	43	1.24	10.21
"	44	1.48	12.30	5.XII	46	1.48	17.39
"	42	1.42	11.93	"	45	1.45	17.35
"	48	1.56	15.13	"	44	1.46	16.51
"	42	1.43	14.91	"	42	1.49	13.04
22.XII	40	1.48	13.20				
"	47	1.50	17.07	*1967*			
"	45	1.50	13.74	27.II	44	1.44	16.13
"	47	1.53	17.32	"	47	1.52	16.26
"	44	1.43	10.96	"	46	—	19.13
"	48	1.53	16.37	"	49	—	22.39
"	47	1.48	15.35	"	51	—	23.82
"	43	1.38	18.46	"	45	—	17.96
				"	44	—	14.63
1965				"	43	—	15.28
25.I	47	1.46	17.53	14.III	49	—	19.29
"	46	1.46	19.16	"	47	—	22.01
"	47	1.56	16.82	"	44	—	17.81
"	41	1.40	16.15	"	42	—	18.28
"	46	1.54	18.77	"	47	—	19.99
"	45	1.50	19.75	"	45	—	20.53
"	45	1.41	13.98	"	45	—	20.00
"	47	1.48	17.72	"	49	—	19.48
"	43	1.42	15.05	"	45	—	16.95
"	43	1.40	17.82	"	50	—	20.61
16.III	48	1.55	19.35	"	48	—	16.69
"	44	1.50	21.69	"	45	—	19.56
"	49	1.59	21.10	"	48	—	21.76
"	47	1.49	16.68	"	47	—	17.71
"	44	1.63	18.66	"	45	—	22.10
"	45	1.53	17.67	31.III	49*	1.90	25.03
"	47	1.59	21.56	"	—*	1.87	—
"	48	1.56	17.51	"	48*	—	26.07
"	43	1.45	19.80	"	53*	—	30.65
"	47	1.53	21.21	"	47*	—	25.36
"	41	1.42	11.42	"	44*	—	17.07
"	42	1.47	18.09	"	41*	—	16.93
5.IV	43	1.55	—	"	48*	—	25.49
"	44*	1.74	—	"	45*	—	21.45
"	44*	1.64	—	"	45*	—	19.91
"	50*	1.84	—	"	45*	—	22.70
"	50*	1.64	—	"	47*	—	25.20
"	47*	1.66	—	"	44*	—	20.83
"	43*	1.61	—	14.IV	48*	1.62	22.83
12.IV	43	1.47	—	"	45*	1.61	19.93
"	45*	1.66	—				
2.V	33*	1.78	—				
"	31*	—	20.54				

O RIPENING AND RIPE OVA (0.5—1.3 mm and 1.3—1.8 mm resp.)
● UNRIPE OVA (> 0.25 ≤ 0.5 mm)
+   „   „   (< 0.25 mm)
⊙ MEAN RIPENING INDEX
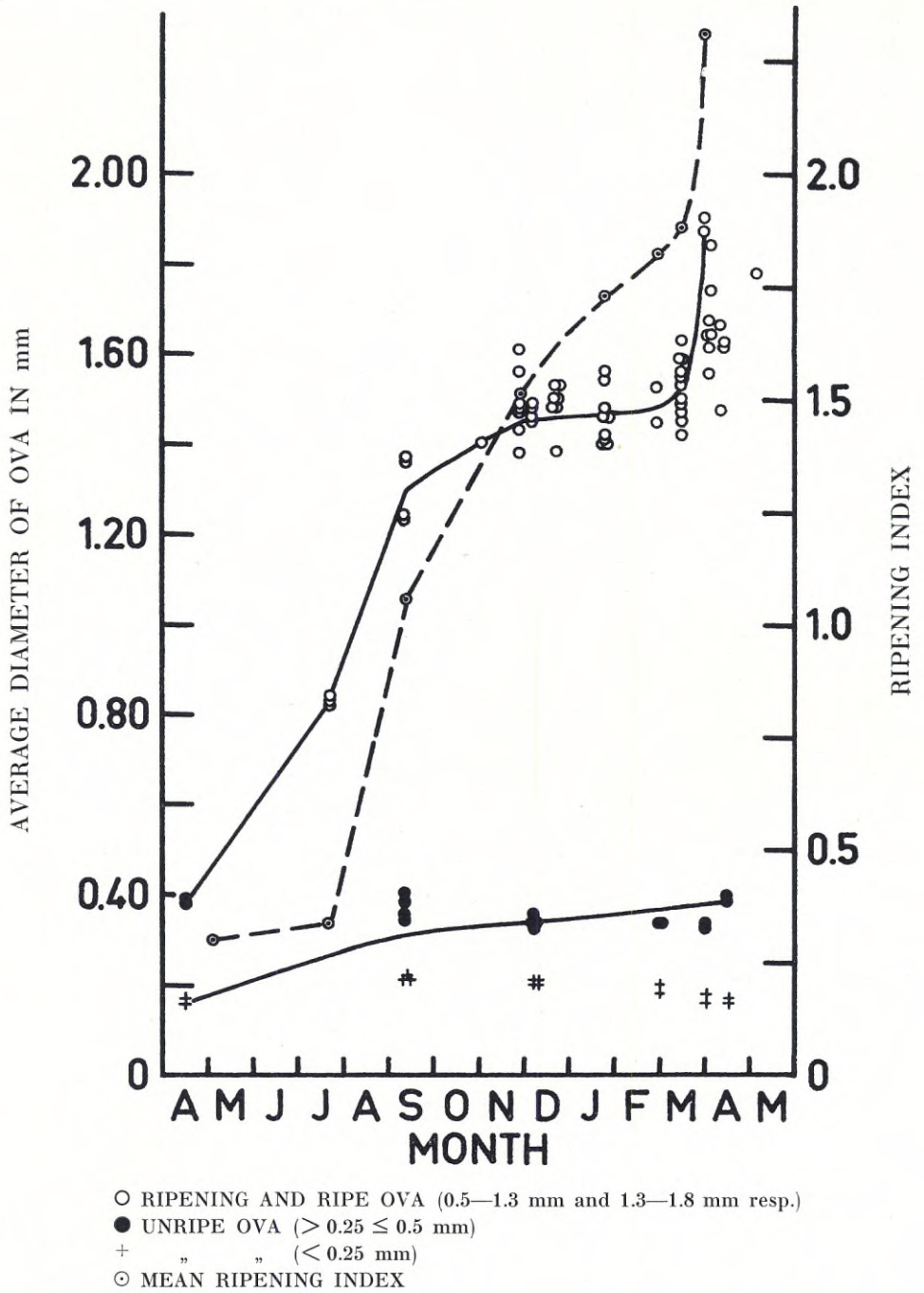
Fig. 1. Egg size vs. ripening index of ripening female ides.
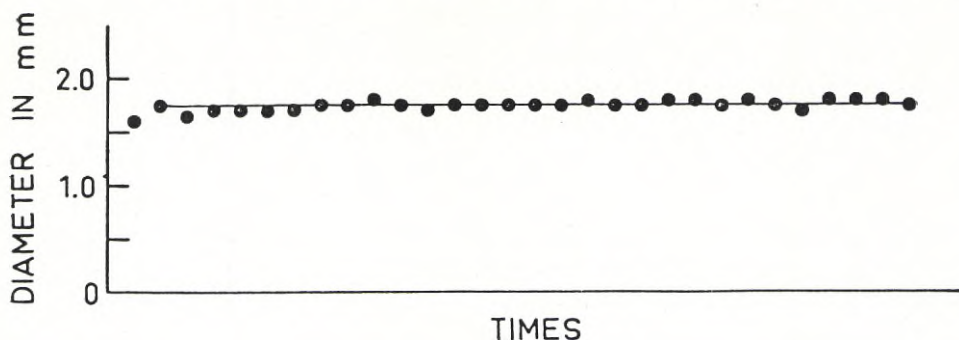
Fig. 2. Sequence of measurements of the diameter of one ide egg submerged in tap water and measured at 1 minute intervals.

that they have just prior to spawning or when the egg becomes ripe. The mean diameter on 27 November was 1.48 mm (n=10 females) and on 16 March 1.53 mm (n=12). The diameter of the ripe eggs on April differs from that of eggs at the end of November only by about 0.22 mm.

According to DRYAGIN (cited by BERG 1949) the eggs from ide from lake Ilmen have a diameter of 1.6—2.2 mm before fertilization and 2.1—2.3 mm after fertilization. POPESCU et al. (1958 and 1960) record a diameter of 1.2—1.6 mm before fertilization and 2.1—2.3 mm after fertilization.

Ripening index

The seasonal development of the gonads can be indicated by a mean ripening index based on fish collected at different times of the year. The ripening index is calculated as the gonad weight×100 divided by the body weight (VLADYKOV 1956). The index was calculated for each fish, and the averages plotted by date to ascertain the seasonal development of the ovaries (Table 2, Fig. 1). Development of the ovary begins in June and reaches a peak in April or just prior to the spawning when the eggs are ripe. There is a resting period just after the spawning. The cycle coincides with the changes of the diameter of the ova: the higher the index, the higher the degree of ripeness. There is some evidence that the males ripen earlier in the season than the females do. In November the testes change from reddish to whitish appearence indicating the presence of spermatozoa. It further seems that older (or larger) fish ripen earlier in the season than do those which are smaller or spawn by the first time. This is in accordance with the first appearence of the males on spawning grounds and also with the fact that the largest ide spawn first (CALA 1970 a).

At the peak of the sexual development, the testes amount to about 1.8 % of the body weight of the fish. In the female the corresponding value for the

ovary is about 21 % of the body weight ranging between 17—30 %. It seems that in young fish a smaller proportion of the body weight relates to egg production than in older fish.

Fecundity

The fecundity of fish is defined as the number of ripening eggs found in the ovaries prior to spawning. As mentioned above (*vide* p. 34) before the onset of the spawning season the ovaries contain three kinds of developing egg. Two kinds are minute (both contained in group (1), p. 34, ≤ 0.5 mm) and develop in subsequent years, while the third set, measuring at least 1.3 mm in diameter, will be shed in the coming breeding season. Only the latter eggs are counted when the fecundity is determined.

Data for the present study were collected prior to the spawning run in 1967 from 52 ide females from the River Kävlingeån. Total length and weight of each fish were measured to the nearest millimetre and gram, respectively. The gonads were removed as soon as possible, weighed and preserved in modified Gilson's Fluid (SIMPSON, cited by BAGENAL 1966), consisting of 100 ml 60 % alcohol, 15 ml 80 % nitric acid, 18 ml glacial acetic acid, 880 ml water, and 20 g mercuric chloride. The fluid preserved and hardened the eggs and helped to liberate them by breaking down the ovarian tissue. The jars in which the pair of ovaries from each fish were stored were shaken intermittently during at least one week. Before the eggs were counted the ovarian tissue was removed and clumps of adhering eggs were carefully broken up. The eggs were repeatedly washed with water, which removed the unripe ova (stage 1) and small pieces of ovarian tissue but did not damage the eggs provided they had been sufficiently hardened. Then the material was subsampled.

The eggs were transferred to a filter paper tray, where they were air dried. Of this material two lots of 200 eggs were counted and weighed as well as the total. The total number of eggs was calculated. This is called the SIMPSON's dry *subsampling method* (BAGENAL 1968).

The error of the dry method was tested as follows. 25 subsamples of 200 air dried eggs were weighed from the same pair of ovaries (Table 3). The highest weight was 0.1531 g and the lowest 0.1511 g, mean 0.152 ± 0.0008.

The distribution of the number of large ripening ova ($\geqslant 1.3$ mm in diameter) between the right and left ovaries was often unequal. Of the material examined (30 females) 17 had a larger right ovary, 10 had a larger left ovary, and 3 had ovaries of approximately equal size (Fig. 3). It was considered desirable, therefore, to use the total number of ripening ova in the female to examine the relationship between fecundity and size of the fish (Table 4). The total lengths of the fish ranged from 31.5 to 53.0 cm, mean 45.5,

Table 3. Weights of 25 subsamples of 200 eggs each from the same ide ovary for estimating the error of the dry subsampling method for calculation of the total number of eggs.

0.1519	0.1528	0.1527
0.1519	0.1515	0.1520
0.1521	0.1520	0.1523
0.1514	0.1522	0.1528
0.1516	0.1517	0.1524
0.1514	0.1516	0.1528
0.1516	0.1531	0.1511
0.1527	0.1522	
0.1522	0.1518	

Mean . . . . 0.15207 g

s . . . . ± 0.00077
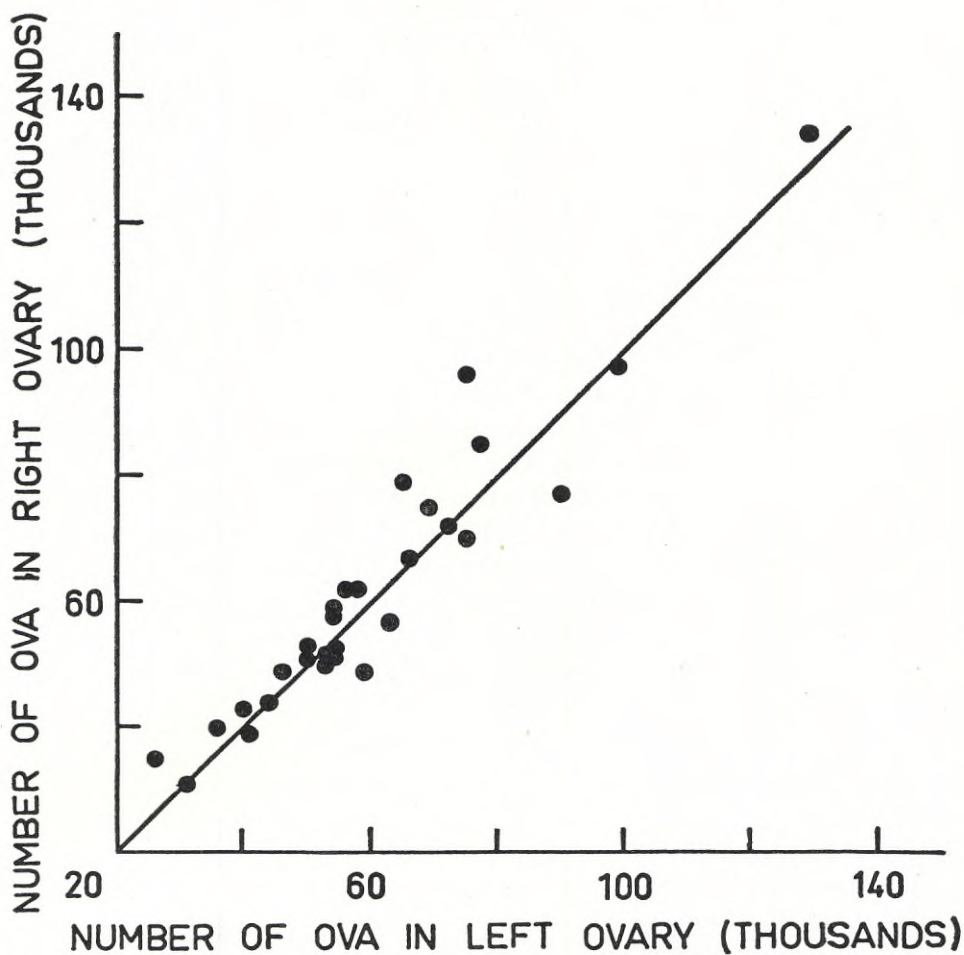
Fig. 3. A comparison of the number of ripe ova in the right ovary with the number of ripe ova in the left ovary from 30 ide from River Kävlingeån. (The diagonal line indicates equal numbers of mature ova in both ovaries.)

Table 4. Fecundity (number of ripe eggs) of 52 ide in relation to length, weight and age. Fish from the River Kävlingeån, prior to the spawning in 1967.

Total length in cm	Weight in g	Fecun-dity	Age group	Total length in cm	Weight in g	Fecun-dity	Age group
31.5	426	42,279	VII	46.2	1500	120,084	VIII
39.0	780	61,643	VI	46.5	1348	87,990	VIII
39.7	877	75,945	VIII	46.5	1659	195,838	VIII
41.0	936	83,014	VI	46.5	1380	129,788	IX
41.5	827	60,739	X	46.5	1499	132,754	IX
41.5	997	79,538	VII	46.7	1481	154,119	IX
42.0	963	108,180	VII	47.0	1560	132,951	X
43.2	1201	89,129	IX	47.0	1446	125,316	XI
43.5	1088	94,397	IX	47.2	1327	122,194	VIII
43.5	1250	112,759	IX	47.3	1313	107,804	X
44.0	1156	83,527	VIII	47.3	1723	162,335	X
44.0	1305	103,269	VIII	47.5	1516	144,495	X
44.5	1535	119,948	X	47.5	1600	144,313	XI
44.5	1165	107,105	VIII	47.8	1114	100,965	VII
44.6	1158	110,421	IX	48.0	1500	143,698	IX
44.6	1115	106,232	VII	48.0	1270	104,781	X
44.7	1215	108,230	VIII	48.3	1565	143,709	IX
44.7	1282	105,724	X	48.4	1484	147,664	VIII
45.0	1390	145,453	VIII	48.5	1729	166,374	XI
45.0	1376	112,190	VIII	48.6	1540	144,878	X
45.0	1181	104,632	IX	49.2	1633	149,182	X
45.1	1194	111,149	VIII	49.8	1635	117,630	VIII
45.2	1285	129,119	IX	50.0	1705	171,165	VIII
45.3	1280	136,343	VIII	50.5	1669	150,264	X
45.5	1368	102,798	VII	51.5	1885	192,957	XI
45.5	1380	105,783	IX	53.0	2325	263,412	XIV

representing age groups VI through XI and XIV. The total numbers of ripe eggs ranged between 42,279—263,412, approximate mean 122,000.

BERG (1949) estimated the fecundity of the Dnieper ide to between 39,000 and 114,000 eggs, mean 88,000. POPESCU et al. (1960) reported the number of eggs from 30 females of the lower Danube ide to be 15,000—125,000; the fish had a total lengths between 28.8 and 48.3 cm and represented age groups III—VII and IX.

A scatter diagram of the number of eggs plotted against the total length (Fig. 4) of the fish gives a relation expressed by the formula:

$$\log F = -3.63017 + 3.4358 \log L$$

where F=number of eggs produced and L=total length in cm. Hence, the mean number of eggs per female increased from about 27,000 eggs for a 30 cm female to about 161,000 eggs for a 50 cm female, or, 7,814 eggs for each increase in body length of 1 cm within the range of 31.5—53.0 cm.

The relation of body weight can be described by a straight line (Fig. 5), with the mean number of eggs increasing from approximately 30,000 for a 500 g female to about 193,000 for a 2,000 g female, i.e. the fecundity increased by about 53,000 eggs for each increase of body weight of 0.5 kg

Fig. 4. Number of ripe ova in relation to the total length. River Kävlingeån, 1967.

within the range 0.5—2 kg (or approximately 100 eggs for each increase of weight of 1 g). This relation is expressed by the formula:

$$F = -25.4262 + 0.1094\ W$$

where F=number of eggs produced and W=body weight in grams. A similar relation was made of the number of ripe ova to the age and to the total weight of the ovary of the fish (Figs. 6 and 7). The linear relations were expressed by the formula:

$$F = -99.6154 + 25.2074\ A$$
$$\text{and } F = 44.5508 + 0.2721\ X$$

where F=number of eggs produced, A=age of the fish and X=weight of the ovary in grams.

$$F = -25.4262 + 0.10946 \ W$$
$$r = 0.913$$
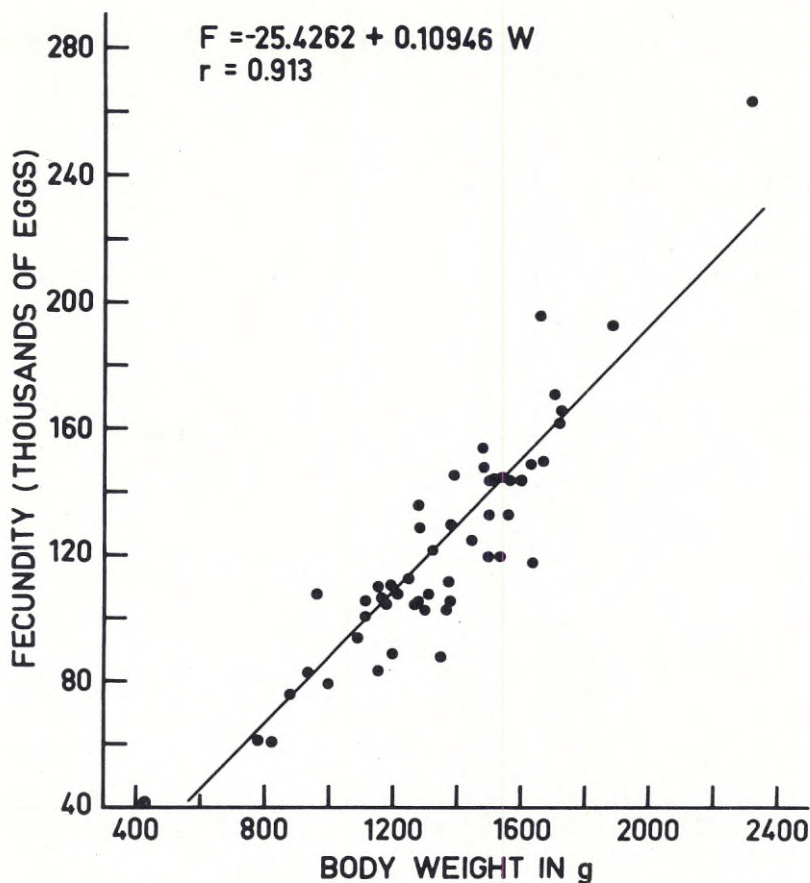
Fig. 5. Number of ripe ova in relation to body weight. River Kävlingeån, 1967.

From the correlations of fecundity and body length (r=0.885), body weight (r=0.913), age (r=0.783) and ovary weight (r=0.799) it may be deduced that the egg number agreed more closely with body weight than with length, ovary weight, of age.

IV. Acknowledgments
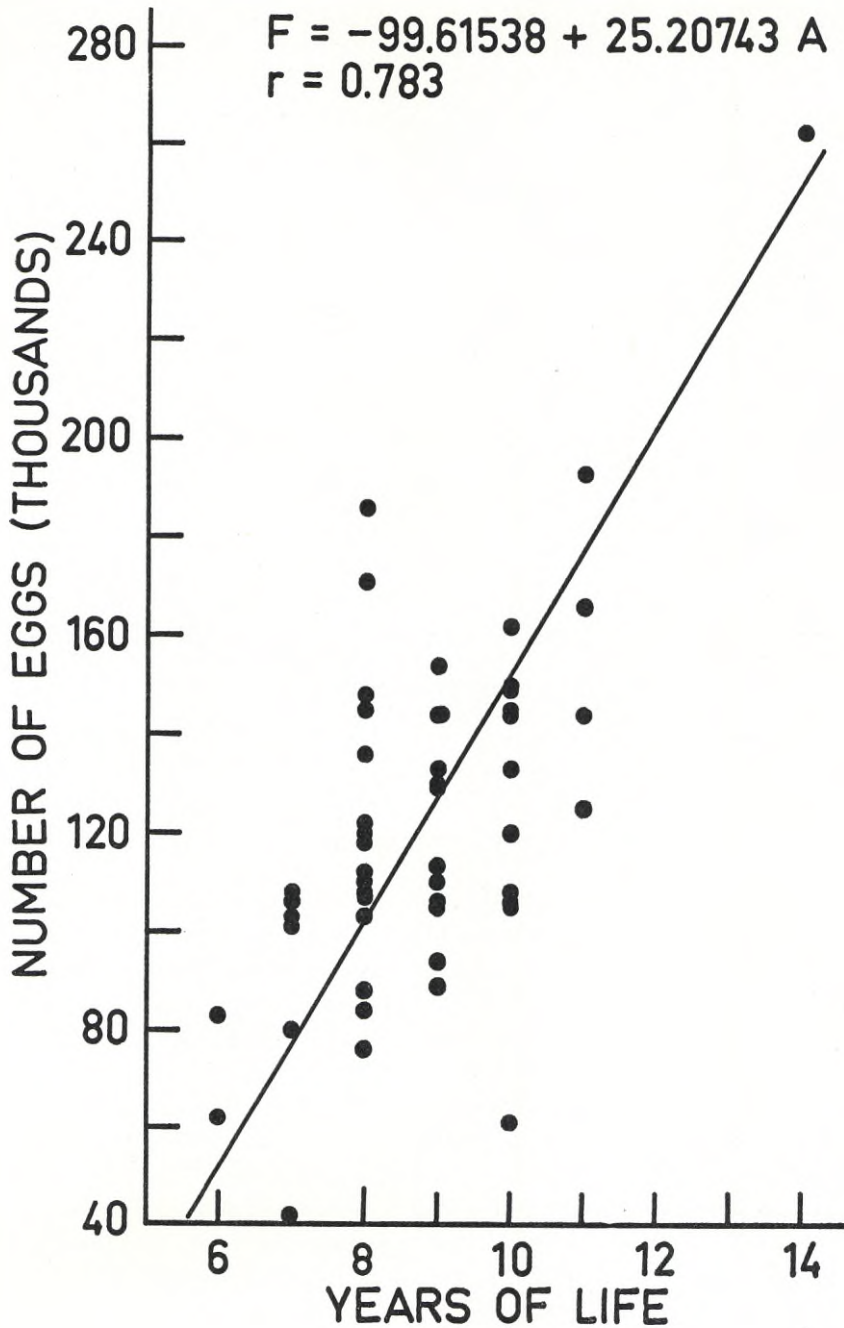
Fig. 6. Number of ripe ova in relation to the age of the ide. River Kävlingeån, 1967.
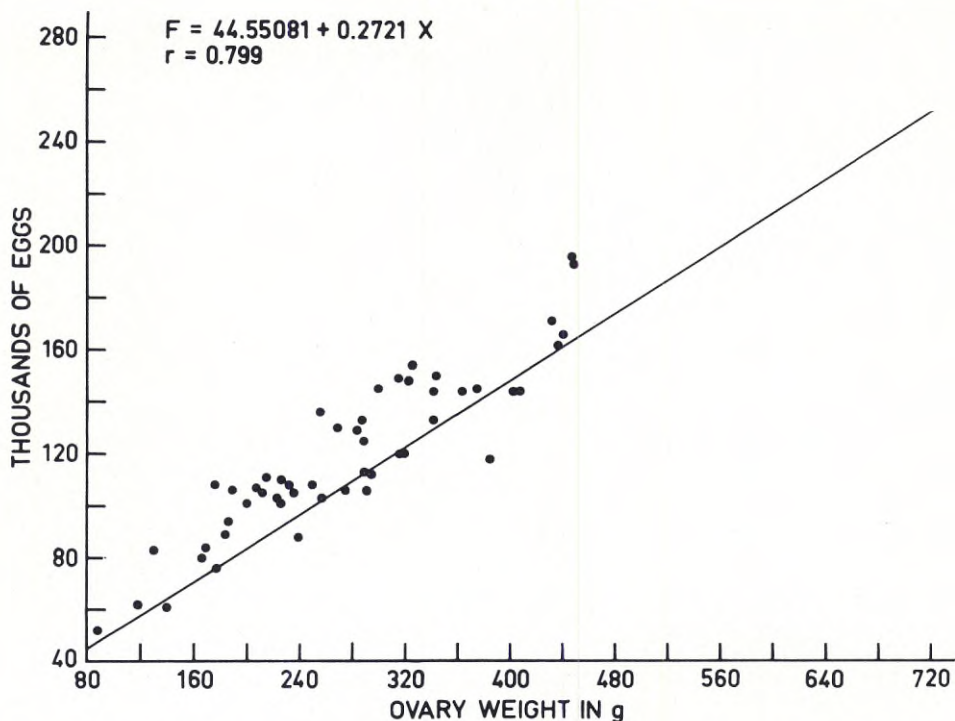
Fig. 7. Number of ripe ova in relation to the ovary weight. River Kävlingeån, 1967.

VI. Summary

An examination of size and age at maturity, ripening and fecundity was made of ide from the lower part of River Kävlingeån from November 1964 to spring 1967. Fish with well developed gonads apparently capable of producing gametes during the current year were considered to be mature.

All ide shorter than 31.5 cm in total length were immature, and all longer than 43.1 cm were mature (Table 1). The shortest mature male was 39.2 cm long. All males were mature at lengths greater than 40.1 cm.

The first mature females appeared at 30.9—32.8 cm (shortest mature individual measured 31.5 cm). All females longer than 43.1 cm were mature. Males reached 100 % maturity at a length 3 cm less than the females.

All ide younger than age group VI were immature and all older than the VII age group were mature. All males older than age group VI were mature (*vide* Table 1).

Ripening females (2 weeks before the spawning) contained eggs in three stages of development: 1 a) unripe: 100—250 μm diameter, clear, nucleated egg cells; 1 b) unripe: 300—500 μm diameter, oil globule vaguely discernible, especially in the largest ova, egg with clouded appearence; 2) ripening: 0.5—

1.3 mm diameter; and 3) ripe: 1.30—1.85 mm diameter, mean 1.50. The eggs ready to be laid and fertilized have a mean diameter of about 1.70 mm. 24 hours after the eggs have been deposited they have a mean diameter of about 2.3 mm (Table 2 and Fig. 1).

Females that would be ripe in April (spawning time) can be distinguished from immature females as early as in the previous July on the basis of examining the mean diameter of 30 of the largest ova (Table 2 and Fig. 1). The largest increase in diameter of the ova occurs in August when the eggs have reached a mean diameter of about 1.30 mm in the middle of the month. In November the ova have the size that they have just prior to spawning or when the egg becomes ripe.

The higher the ripening index, the higher the degree of ripeness. There is some evidence that the males ripen earlier in the season than the females do. It further seems that older (or larger) fish ripen earlier in the season than do those which are smaller or spawn by the first time. This in accordance with the first appearance of the males on spawning grounds and also with the fact that the largest ide spawn first (CALA 1970 a).

The total numbers of ripe eggs ranged between 42,279—263,412, approximate mean 122,000. A scatter diagram of the number of eggs plotted against the total length (Fig. 4) of the fish gives a relation expressed by the formula:

$$\log F = -3.63017 + 3.4358 \log L$$

The relation of body weight can be described by a straight line (Fig. 5), with the mean number of eggs increasing from approximately 30,000 for a 500 g female to about 193,000 for a 2,000 g female, *i.e.* the fecundity increased by about 53,000 eggs for each increase of body weight of 0.5 kg within the range 0.5—2 kg. This relation is expressed by the formula:
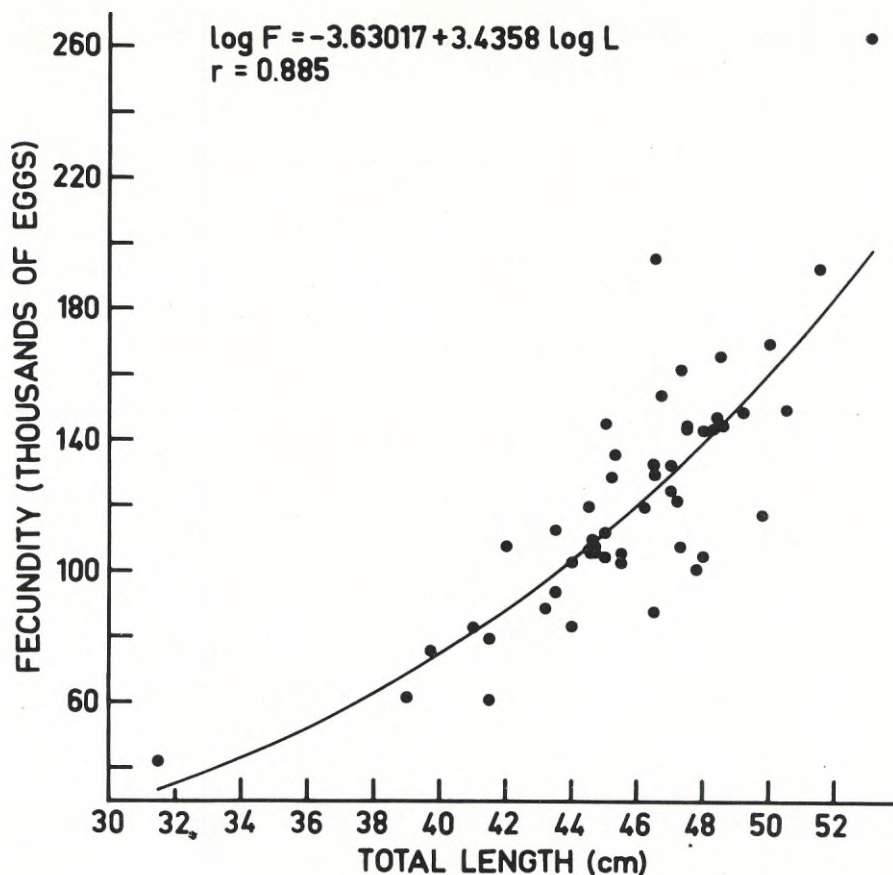
$$F = -25.4262 + 0.1094 \, W \quad (F = \text{number of eggs and } W = \text{body weight})$$

A similar relation was made of the number of ripe ova to the age and to the total weight of the ovary of the fish (Figs. 6 and 7). The linear relations were expressed by the formula:

$$F = -99.6154 + 25.2074 \, A$$
$$\text{and } F = 44.5508 + 0.2721 \, X$$

where F = number of eggs, A = age of the fish and X = weight of the ovary.

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Zur Biologie und Populationsdynamik von Polyartemia forcipata (Fischer)[1]

Von Bengt Göran Hellström[2] und Arnold Nauwerck[3]

I. Einleitung

Auf der Suche nach geeigneten Fischfutter-Organismen zum Aufbau einer idealen Nahrungskette im See Latnjajaure (Nauwerck 1967) richtete sich unser Interesse auf folgende Arten: *Lepidurus arcticus* Pallas, *Branchinecta paludosa* (O.F.M.), *Polyartemia forcipata* (Fischer), *Gammarus lacustris* Sars, *Asellus aquaticus* (L.) und *Mysis relicta* Lovén. Alle diese Arten schienen im Prinzip geeignet, die bodengebundene Primärproduktion des Sees (Bodin & Nauwerck 1968) für Fische besser nutzbar zu machen. Die ersten drei von ihnen kommen in näherer oder nächster Umgebung des Sees vor. Die vorliegende Arbeit diente der Untersuchung der im Abisko-Gebiet in kleineren Gewässern weit verbreiteten *Polyartemia forcipata*. Wenngleich *Polyartemia* nicht alle Bedingungen für einen idealen Fischfutter-Organismus zu erfüllen scheint, sind unsere Erfahrungen (ausführlicher bei Hellström 1970) von genügendum Interesse, um hier mitgeteilt zu werden. Die erste, kurze Beschreibung von *Polyartemia forcipata* gibt Fischer (1851). Eine ausführlichere Beschreibung, die auch die allgemeine Biologie der Art umfasst, folgt bei Sars (1896). Später war sie Gegenstand vergleichender Studien durch Ekman (1902), Wesenberg-Lund (1939) und Linder (1941). Das subarktische Verbreitungsgebiet der Art macht die geringe Aufmerksamkeit verständlich, die ihr bisher geschenkt wurde.

Ausser einer einzigen Abbildung bei Sars fehlen Hinweise über Larvalentwicklung und Aussehen der Jugendstadien. Während der kurzen eisfreien Periode der Wohngewässer der Art wurden stets nur adulte Tiere beobachtet. Die Entwicklung vom (Dauer-) Ei zum adulten Tier geschieht nach Linder „wahrscheinlich schon unter dem Eis". Viel mehr ist über die Biologie der Art nicht bekannt.

II. Material und Methoden

Aus drei Tümpeln ca. 2 km SE der Station Latnjajaure am Südabhang des Latnjatjårro („Övre Tretjärn", „Mellersta Tretjärn" und „Nedre Tretjärn")

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wurden vom 27. Juni bis zum 17. September 1969 durchschnittlich jeden dritten bis vierten Tag Proben entnommen. Die drei Tümpel liegen auf ca. 1000 m Höhe in der niederalpinen Region, stehen nicht in gegenseitiger Verbindung und stellen den höchstgelegenen bisherigen Fundort für Polyartemia im Abisko-Gebiet dar.

Mit einem Planktonnetz mit der Maschenweite 63 µ wurden qualitative Proben entnommen und mit Formalin fixiert. Insgesamt wurden reichlich 2500 Tiere von 26 Probenahmedaten vermessen. Zeichnungen verschiedener Stadien wurden mit dem Zeichenapparat hergestellt.

Gewichtsbestimmungen konnten mangels einer empfindlichen Waage erst nach Rückkunft nach Uppsala und nur an fixiertem Material durchgeführt werden. Zur Bestimmung des Frischgewichts wurden die Tiere auf Filtrierpapier äusserlich abgetrocknet, danach fur 24 Stunden bei 60°C deponiert und anschliessend das Trockengewicht bestimmt. Für jede Wägung wurden 10 erwachsene Tiere verwandt.

An je etwa 10—20 Tieren beiderlei Geschlechts von drei über die Saison verteilten Daten wurden Untersuchungen des Darminhalts vorgenommen. Dabei wurde der Darm unter der Lupe freipräpariert, unter dem Mikroskop untersucht und Zusammensetzung, Menge und Zustand der aufgenommenen Nahrung notiert.

Um ein Mass für den Energieverbrauch der Tiere zu gewinnen, wurden an erwachsenen Tieren einige einfachen Respirationsversuche durchgefuhrt. Da die Versuche an der Station Latnjajaure ohne spezielle technische Hilfsmittel durchgeführt werden mussten, konnte nur bei drei einigermassen konstanten Temperaturen gearbeitet werden, nämlich 1°C im Schnee, 8°C im See Latnjajaure und 19°C im Hause. Die beiden ersten Temperaturen variierten kaum, die letzte nicht mehr als ±0,5°C.

Die Versuchstiere wurden über Nacht an die Versuchstemperatur gewöhnt, sodann zu je 5 Exemplaren in 100-ml-Flaschen gebracht und in drei Parallelen 10—15 Stunden exponiert. Alle Versuche wurden mit Wasser aus dem See Latnjajaure durchgeführt. Die Versuchszeiten wurden aufgrund von Vorversuchen gewählt, die ergaben, dass messbare O_2-Abnahmen bei der gewählten Besatzdichte erst nach mehreren Stunden eintreten.

III. Resultate

Der Lebenscyklus von *Polyartemia*

Die postembryonale Entwicklung

Der kleinste gefundene Larventypus ist in Fig. 1 a wiedergegeben. Die zweiten Antennen sind wohl entwickelt, ebenso die Mandibularfüsse, die als Schwimmorgane dienen. Auffällig ist, dass die Komplexaugen schon unmittel-
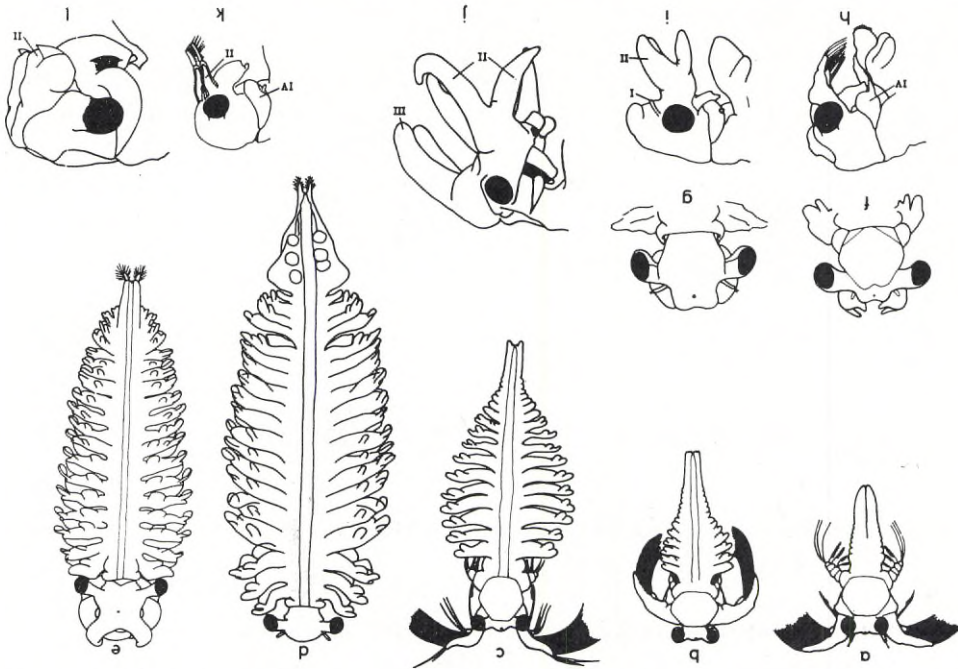
Fig. 1. *Polyartemia forcipata.* a—c, f—i, k Larvenstadien (a=1,2 mm, b=1,6 mm, c=
2,5 mm); d, l Weibchen (12,6 mm); e, j Männchen (9,9 mm); f—j und k, l Umbildung der
Kopfregion beim Männchen und beim Weibchen; I=1. Antenne, II=2. Antenne, III=
Frontalbeihang, IV=Mandibeln.

bar nach dem Schlüpfen ausgebildet sind, im Gegensatz z.B. zu *Branchinecta,*
bei der anfangs nur das Naupliusauge ausgebildet ist (SARS 1896). Die Fuss-
anlagen, am vorderen Teil des Thorax am deutlichsten ausgebildet, erscheinen
als kleine Ausbuchtungen entlang dem Körper. Die Beine entwickeln sich
dann successiv von vorn nach hinten und übernehmen nach und nach die
Schwimmfunktionen der Antennen und der Mandibularfüsse.

Bei der Zurückbildung der Mandibularfüsse schmilzt die Anzahl ihrer
Glieder zusammen und die Füsse verschwinden schliesslich ganz (Fig. 1 a—c,
f, g, k). Die Grösse der Mandibeln bleibt hingegen offensichtlich von der
Larve bis zum erwachsenen Tier fast unverändert.

Die zweiten Antennen werden zurückgebildet (Fig. 1 b—c) und beim
Männchen zu dreigeteilten Greifwerkzeugen umgestaltet (Fig. 1 f, g, j). Wenn
das Tier eine Länge von ca. 4 mm erreicht hat (Fig. 1 f) beginnt die Heraus-
bildung des Stirnanhangs, etwa paralell mit der des dritten Lappens des
Greiforgans. Mit etwa 7 mm Länge erreichen die Tiere Geschlechtsreife und
beginnen zu kopulieren. Ein erwachsenes Männchen zeigt Fig. 1 e.

Fig. 1 k zeigt ein Zwischenstadium der Zurückbildung der zweiten Antennen
beim Weibchen. Wenn dieses etwa 6 mm lang ist, beginnen die Antennen

4
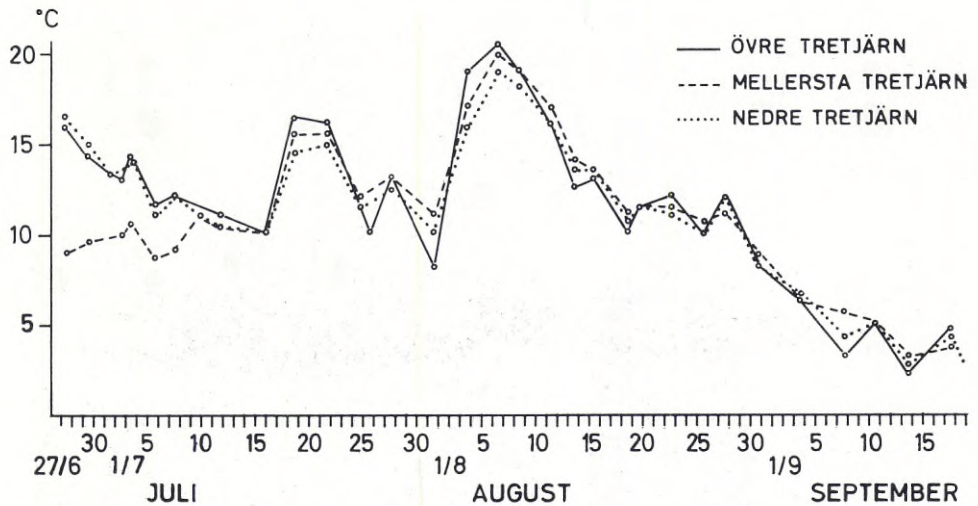
Fig. 2. Wassertemperaturen in Övre, Mellersta und Nedre Tretjärn Juni—September 1969.

sich mehr und mehr zu verkürzen und werden schliesslich dick und kräftig, mit einer dreikantigen Spitze am Ende (Fig. 1 e). Ungefähr im gleichen Zeitraum wächst die Eikapsel aus und ist fertig entwickelt, wenn die Tiere mit etwa 8—9 mm Länge Geschlechtsreife erreicht haben. Ein erwachsenes Weibchen zeigt Fig. 2 d.

Kopulation und Eibildung

Im Övre Tretjärn wurden am 2. Juli grosse Mengen kopulierender Paare beobachtet. 5 Tage später waren die ersten fertigen Eier frei im Wasser zu finden. Die Entwicklungszeit der Eier, gerechnet vom Zeitpunkt ihrer Anlage bis zum Zeitpunkt ihrer Ablage, dürfte etwas länger sein, da die grosse Zahl der kopulierenden Paare am 2. Juli wahrscheinlich macht, dass die ersten geschlechtsreifen Tiere schon etwas früher auftraten. Immerhin waren am 29. Juni noch keine kopulierenden Paare anzutreffen. Die mittlere Wassertemperatur während der 5 Tage war 12,7°C (Fig. 2).

Im Nedre Tretjärn wurden die ersten kopulierenden Paare am 3. Juli beobachtet (Abb. 1) 8 Tage später die ersten Eier. Die mittlere Wassertemperatur während dieser Zeit war 11,7°C. Im Mellersta Tretjärn herrschten vergleichbare Temperaturen erst nach Abschmelzen eines lokalen Schneefelds. Die ersten kopulierenden Paare erschienen hier am 11. Juli, die ersten Eier 7 Tage später. Die mittlere Wassertemperatur während dieser Periode war 12,0°C. Die Durchschnittslänge der Tiere bei Beginn der Kopulation war in allen drei Gewässern die gleiche. Eier beginnen aufzutreten, wenn die Weibchen etwa 8 mm lang sind. Mit zunehmender Länge der Weibchen nimmt
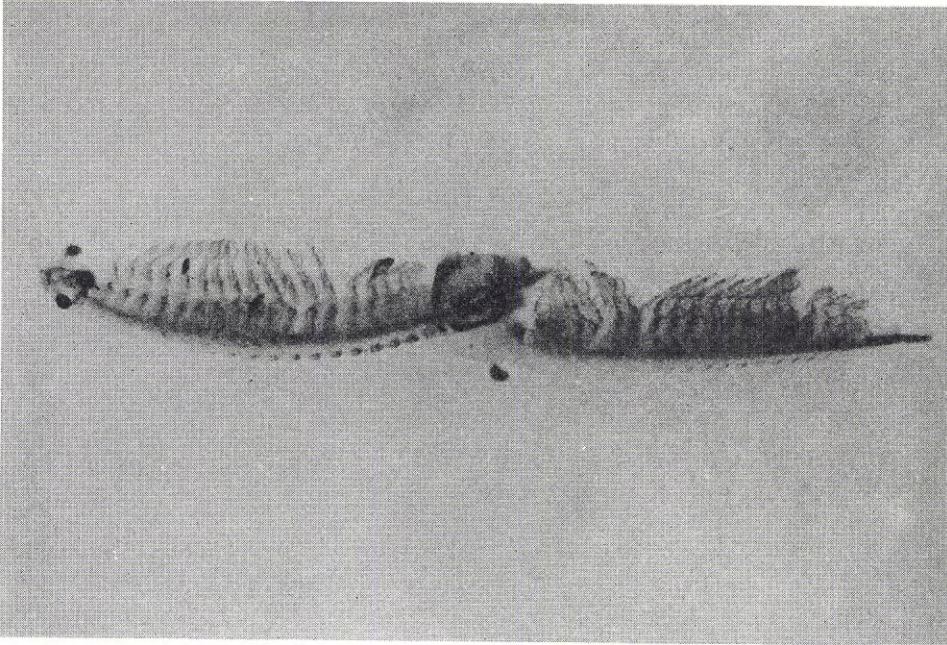
Abb. 1. *Polyartemia forcipata*. Kopulierendes Paar. Das Photo zeigt deutlich die Schwimm-
bewegung der Tiere.

auch die Anzahl der Eier in den Eikapseln zu (Fig. 3). Indessen variiert die
Eizahl pro Weibchen stark innerhalb ein und derselben Längenklasse. Dies
erklärt sich aus dem Verlauf der Eientwicklung: die zunächst angelegte Zahl
von Eiern ist abhängig von der Länge des Tieres. Die Eier entwickeln sich
aber nicht gleichzeitig, sondern so, dass die der Oviduktöffnung am nächsten
gelegenen zuerst, die am entferntesten gelegenen zuletzt reifen. Die fertigen
Eier werden der Reihe nach abgelegt, nachdem sie in der Drüsenmasse im
unteren Teil der Eikapsel mit einer harten Schale umgeben wurden. Erst
Nachdem der obere Teil der Eikapsel ganz von Eiern geleert ist, werden
neue Eier angelegt.

Diese Beobachtung sowie die Tatsache, dass praktisch die ganze Population
vom Erreichen der Geschlechtsreife Anfang Juli bis zu ihrem Verschwinden
einige Wochen vor der Eislegung (25. September) ununterbrochen in Paarung
begriffen war, erlaubt sicher die Annahme, dass jedes Gelege eine neue
Befruchtung erfordert. Das Fehlen eines *receptaculum seminis* beim Weib-
chen sowie die von denjenigen der Weibchen nicht unterschiedene Lebens-
dauer der Männchen lassen sich im gleichen Sinne deuten. Dass die Anzahl
der Männchen die der Weibchen um reichlich 10 % überwiegt, tut ein Übriges
zur Sicherstellung ständig neuer Befruchtungen.

Bemerkenswert, ist dass die geschlechtsreifen Weibchen gleichzeitig mit
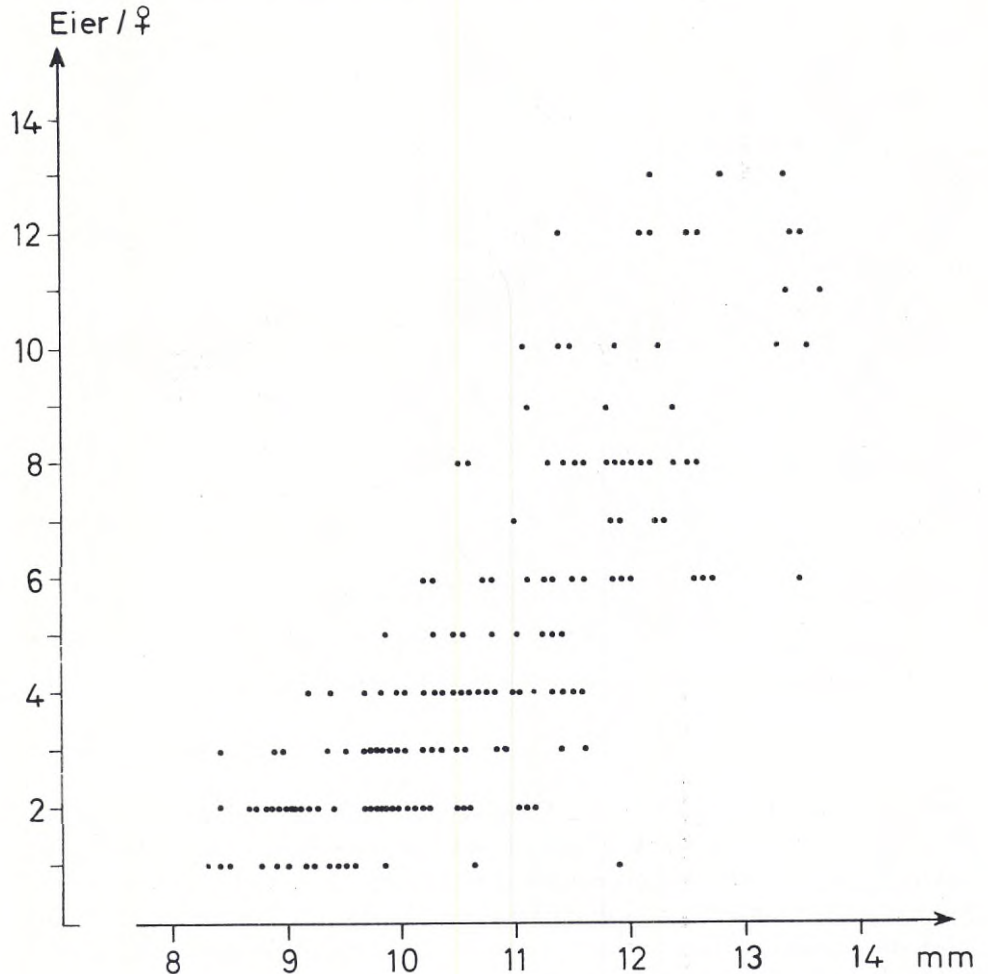
Fig. 3. *Polyartemia forcipata*. Eizahlen im Verhältnis zur Grösse der Weibchen.

der ersten Eianlage einen dunkelbauen Fleck auf der Eikapsel ausbilden. Es ist nicht ausgeschlossen, dass dieser Fleck den Männchen zur Orientierung dient.

Der Zuwachs der Adulten

Nach Erreichen der Geschlechtsreife wachsen die Tiere weiter, zuerst ziemlich schnell, dann mit abnehmender Geschwindigkeit (Fig. 4 und 5). Die durchschnittliche Endlänge ist 12,2 mm für die Weibchen und 10,5 mm für die Männchen im Mellersta Tretjärn und 12,0 mm bzw. 9,8 mm im Nedre Tretjärn. Die Werte im Övre Tretjärn, 12,6 mm und 11,0 mm, sind nicht
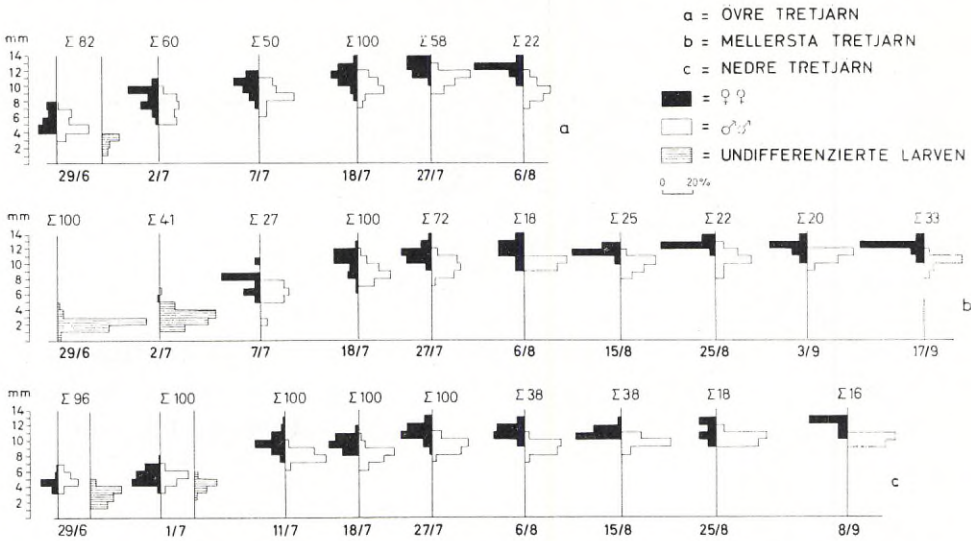
Fig. 4. *Polyartemia forcipata.* Prozentuale Verteilung verschiedener Längenklassen in Övre, Mellersta und Nedre Tretjärn 1969.

ganz vergleichbar mit denen aus den zwei erstgenannten Seen. Die Gründe dafür werden in Abschnitt 4.3. behandelt.

Nach den Angaben von SARS (1896) erreichen die Weibchen von Polyartemia bis zu 16 mm, die Männchen bis zu 10 mm Länge. Im vorliegenden Material waren nur zwei Weibchen länger als 14 mm, das grösste Exemplar 14,3 mm, während drei Männchen grösser als 12 mm waren, und auch die mittlere Länge nur im Nedre Tretjärn unter 10 mm lag. Die Längenunterschiede sowohl zwischen den beiden Geschlechtern in ein und demselben Tümpel als auch zwischen Männchen und Weibchen aus den verschiedenen Tümpeln sind statistisch gesichert (HELLSTRÖM 1970).

Dass die Männchen kleiner sind als die Weibchen ist bei vielen Phyllopoden der Fall. Interessanter sind die Grössenunterschiede innerhalb des gleichen Geschlechtes von Biotop zu Biotop. Sicher spielt dabei in erster Linie die Nahrung eine Rolle (vergleiche Seite 59) und höchstwahrscheinlich auch die Temperatur. Unsere Gewässer liegen an der Grenze des Verbreitungsgebiets von *Polyartemia*. Höher und mehr arktisch gelegene Fundorte sind uns aus Schwedisch-Lappland nicht bekannt. Man darf also annehemen, dass die Temperatur oder die Nahrung oder beide in unserem Falle im Gegensatz zu den Sars'schen Fundorten für die Art, nahe am Pessimum liegen. Da zwischen unseren Tümpeln ferner praktisch keine Temperaturunterschiede bestehen, darf man annehmen, dass für die hier beobachteten Unterschiede in erster Linie Nahrungsunterschiede verantwortlich sind. Tatsächlich folgt
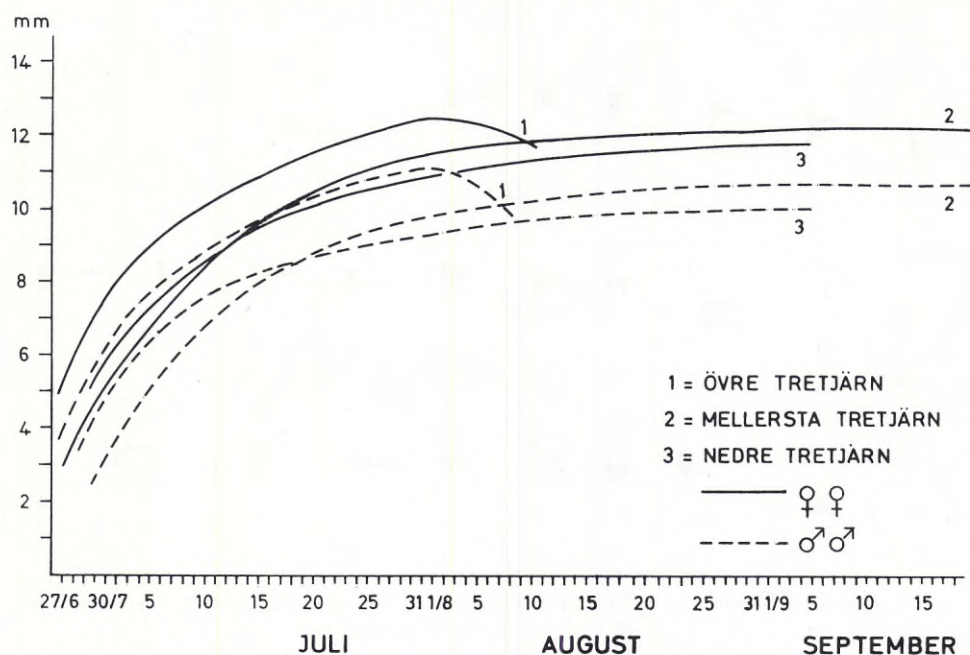
Fig. 5. *Polyartemia forcipata*. Zunahme der mittleren Länge in Övre, Mellersta und Nedre Tretjärn Juni—September 1969.

das Längenverhältnis Weibchen: Männchen dem Nahrungsgradienten nach Abschnitt „Die Nahrung" (Seite 59) (vgl. auch „Respiration"):

	schlechte/wenig Nahrung			gute/viel Nahrung
	M. Tretjärn	N. Tretjärn	Ö. Tretjärn	Sars' Gewässer
L♀ : L♂	1,16	1,23	1,24	1,60

Wir finden also, dass die Männchen bei zunehmend besseren Milieubedingungen relativ und absolut kleiner werden, die Weibchen dagegen relativ und absolut an Grösse zunehmen, wobei die Grössenverhältnisse offenbar in erster Linie von den Nahrungsbedingungen gesteuert werden. Vielleicht darf man in der sichtbaren morphologischen Reduzierung der Männchen den ersten Schritt auf dem Weg zu Zwergmännchen und Parthenogenese sehen, wie ja bei vielen Phyllopoden bei optimalen Nahrungsbedigungen ausschliesslich parthenogenetische Vermehrung vorkommt, wahrend verschlechterte Bedingungen Sexualität auslösen.

Die Populationsdynamik von *Polyartemia*

Die Lebensdauer der Larven

Die fertigen Eier verlassen die Weibchen mit einem durchschnittlichen Durchmesser von 0,45 mm, kleinsten Larven hatten dagegen eine Länge von

0,85 mm. Es wäre demnach möglich, dass uns noch kleinere Larven entgangen sind. Indessen ist diese Möglichkeit nicht sehr wahrscheinlich. Vergleicht man nämlich mit *Asellus aquaticus* (L.) (ANDERSON 1969), so findet man fast die gleichen Grössenverhältnisse: die Eier sind 0,3—0,4 mm gross, die frisch geschlüpften Larven etwa 1 mm lang.

Nachdem Nauplienstadien im strikten Sinne bei *Polyartemia* nicht existieren, sondern die Entwicklung kontinuerlich vor sich geht (innerhalb gewisser Grenzen entwickeln sich verschiedene Organe sogar verschieden schnell bei verschiedenen Individuen) kann die Zeit von Schlüpfen bis zur Geschlechtsdifferenzierung als „Nauplienstadium" betrachtet werden. Die Geschlechtsdifferenzierung tritt damit ein, dass die Antennen des Männchens sich zu teilen beginnen und die Geschlechtsöffnung des Weibchens klar erkennbar wird. Die Tiere sind auf diesem Stadium um 5 mm lang. Da diese Grenze aus den genannten Gründen nicht sehr scharf ist, der Zeitpunkt der Geschlechtsreife dagegen exakt festgelegt werden kann, ist es sinnvoll, nur die Zeit der totalen Larvalentwicklung zu berechnen. Ein Vergleich der Kurven in Fig. 5 mit der Temperatur ergibt bei gewissen Extrapolationen (HELLSTRÖM 1970) folgende Werte:

	Ö. Tretjärn	N. Tretjärn	M. Tretjärn
Entwicklungsdauer	ca. 11 Tage	ca. 14 Tage	ca. 20 Tage
Mittlere Temperatur	15°C	13°C	9°C

Damit ist der Gradient für die Entwicklungsdauer der Larven im Verhältnis zur Temperatur steiler als der für diejenige der Eier (Seite 50). Aus Fig. 2 und 5 lässt sich extrapolieren, dass die ersten Larven 2—3 Wochen vor unseren ersten Probenahmen auftraten, d.h. kurz nach dem Eisbruch bei ca. 4—5°C. Natürlich spielt aber auch die Nahrung bei zunehmender Temperatur eine grössere Rolle.

Die Entwicklungszeit der Larven ist also kurz und derjenigen von Zooplankton in temperierten Gewässern vergleichbar. Mehr als eine Generation Larven werden nicht geboren. *Polyartemia forcipata* ist also einjährig-monocyklisch und bildet ausschliesslich Dauereier.

Die Lebensdauer der Adulten

Nach Fig. 5 ist die Lebensdauer der adulten Tiere im Mellersta Tretjärn ca. 68 Tage und im Nedre Tretjärn ca. 60 Tage, wenn man den Zeitpunkt ihres Verschwindens mit ihrem natürlichen Tod gleichsetzt. Abweichend verhält sich die Population des Övre Tretjärn, die nur 38 Tage erreicht. Die Erklärung hierfür war ein Gehecke von Zwerglumme (*Gavia stellata* L.) an diesem Gewässer. Zwei Junge schlüpften hier um den 20. Juni und begannen ungefähr eine Woche später den *Polyartemia*bestand so effektiv abzugrasen, dass dieser nach zwei weiteren Wochen völlig vernichtet war. Dass die

grössten Exemplare am leichtesten gefangen wurden, zeichnet sich im Absinken der mittleren Grösse der Tiere gegen Ende der Periode deutlich ab.

Die mittlere Lebensdauer der Tiere dürfte unter normalen Verhältnissen in erster Linie eine Funktion der Wassertemperatur sein. Inwieweit die beobachteten Zeiten als normal, lang oder kurz angesehen werden können, lässt sich indessen ohne Vergleichsmaterial nicht beurteilen. Immerhin muss die Lebensdauer im bedeutend wärmeren Sommer 1970 wesentlich kürzer gewesen sein, was daraus hervorgeht, dass die noch im Juli wohl entwickelten Bestände bereits Anfang August völlig verschwunden waren und in keinem der Tümpel mehr ein einziges Exemplar erbeutet werden konnte.

Obwohl nicht versucht wurde, die Absolutbestände zu bestimmen, lässt sich das relative Verhältnis der Populationsgrössen in den drei Gewässern anhand der Zahl der gefangenen Tiere im Verhältnis zu Anzahl und Länge der notwendigen Netzzüge abschätzen. Die „Anstrengungseinheiten" zur Gewinnung etwa der gleichen Anzahl Tiere verhielt sich zwischen Nedre, Övre und Mellersta Tretjärn etwa wie 1 : 2 : 3. Die Bestandsabnahme im Laufe der Saison (HELLSTRÖM 1970) macht deutlich, dass auch in den beiden Gewässern ohne Vogelfrass andere als natürliche Todesursachen, d.h. in erster Linie andere Predatoren (vgl. Abschnitt „Produktionsberechnungen") zu verschieden schneller Reduzierung der Populationen beigetragen haben müssen.

Die Eiproduktion

Wie erwähnt werden die Eier nicht kontinuierlich sondern in Gelegen gebildet, wobei die Gelegegrösse in erster Linie von der Länge des Muttertieres abhängt (Seite 50). Die Entwicklungsdauer der Eier ist eine Temperaturfunktion. Aus Fig. 3 und 5 kann die durchschnittliche Eibestand zu verschiedenen Zeitpunkten ermittelt werden. Die Entwicklungsdauer bei den entsprechenden Temperaturen lässt sich aus einer durch die drei beobachteten Werte (Seite 50) gelegten Kurve entnehmen. Diese Kurve deckt zwar nicht die höchsten im Wasser aktuellen Temperaturen, durch Annehmen von mittleren Temperaturen während gewisser Zeitabschnitte braucht sie indessen nur wenig extrapoliert werden und dürfte in diesem Rahmen brauchbar sein. Damit lassen sich Anzahl Gelege und totale Eiproduktion während der Lebensdauer eines Weibchens ermitteln. Die gewählten Zeitintervalle und die Ergebnisse dieser Berechnung zeigen Tab. 1 und Fig. 6.

In der Regel sind die Durchschnittstemperaturen der drei Gewässer einander so nahe, dass sie für unseren Zweck nicht getrennt zu werden brauchen. Wo dies nötig erscheint, sind die abweichenden Werte in Paranthesen angeführt. Nur in einem Fall wird die Entwicklungszeit in allen drei Gewässern Verschieden Zwischen 10 und 9°C nähert sich die Entwicklungsdauer der Eier rasch Unendlich, d.h. unterhalb 9°C werden keine Eier mehr gebildet.
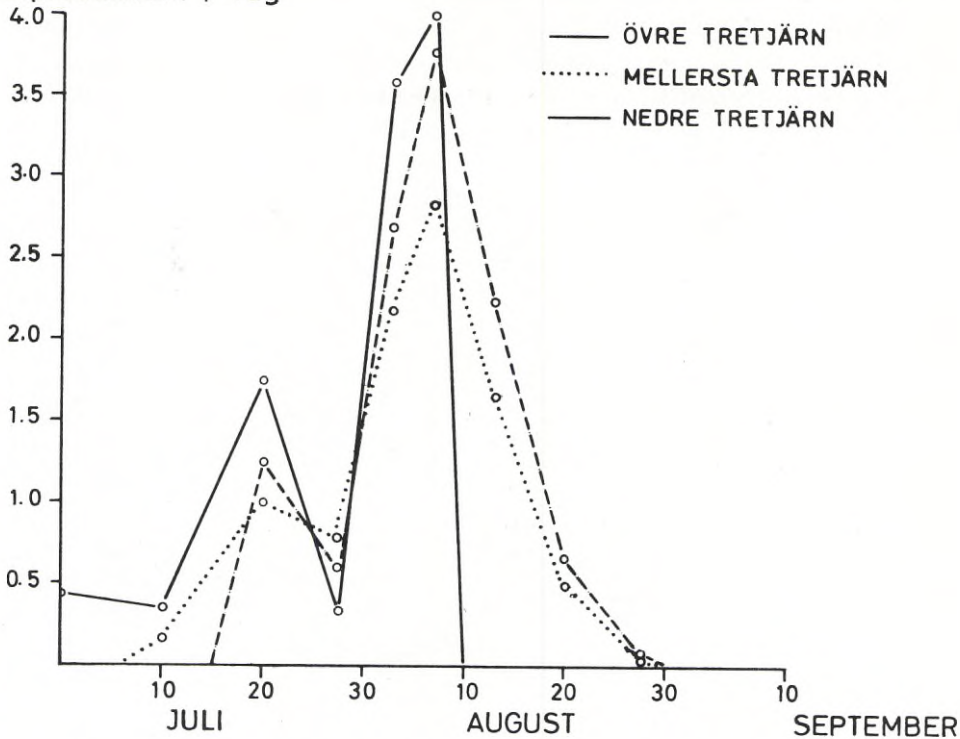
Fig. 6. *Polyartemia forcipata*. Eiproduktion pro Weibchen und Tag in Övre, Mellersta und Nedre Tretjärn Sommer 1969.

Durch Dividieren der Totalzahl produzierter Eier mit der mittleren Anzahl Eier pro Weibchen erhält man annähernd die Zahl der Gelege pro Weibchen. Sie beträgt reichlich 11 (11,1) im Övre Tretjärn, reichlich 10 (10,4) im Nedre Tretjärn und knapp 10 (9,9) in Mellersta Tretjärn. Dank der frühzeitig höheren Temperatur im Övre Tretjärn bleibt die Anzahl der Gelege trotz des vorzeitigen Endes der Population nicht geringer als in den anderen beiden Gewässern. Im Nedre Tretjärn wirkt sich der dichtere Bestand offensichtlich negativ auf die Eiproduktion des einzelnen Weibchens aus (Konkurrenz?), jedoch bleibt die Totalproduktion des Gewässers dank der absoluten Bestandsgrösse die grösste der drei.

Die berechneten Zahlen führen zu folgenden Überlegungen. Wenn man davon ausgeht, dass von jedem Weibchen 2 Eier sich zu erwachsenen Individuen entwickeln müssen, um den Fortbestand der Art zu sichern und in nächsten Jahr die gleiche Populationsgrösse zu garantieren, können 96—97 % der Eier oder Jugendstadien untergehen, ohne dass die Population kleiner wird. Im Hinblick auf die rasche Entwicklung vom Ei zum Adulten und den

Tabelle 1. Die Eiproduktion von *Polyartemia forcipata* in Övre, Mellersta und Nedre Tretjärn Sommer 1969. t=Zeitinterwall; T=durchschnittliche Temperatur (°C) während t; d=Erneuerungszeit der Eier (Tage) bei Temperatur T; t/d=Erneuerungskoeffizient während t; n=durchschnittlicher Bestand Eier/♀ während t; n·t/d=Eiproduktion pro ♀ während t.

t	T	d	t/d	n			n · t/d		
				ÖT	MT	NT	ÖT	MT	NT
25.6— 5.7	14	3,5	2,9	1,8	—	—	4,7	—	—
„ M	9	→ ∞	→ 0	—	—	—	—	—	—
5.7—15.7	11	12	0,8	4,2	2	2	3,4	—	1,6
„ M	9	→ ∞	→ 0	—	—	—	—	—	—
15.7—25.7	13,5	4	2,5	7	—	4	17,5	—	10,0
„ M	13	4	2,5	—	5	—	—	12,5	—
25.7—30.7 Ö	10,5	20	0,2	9	—	—	1,8	—	—
„ M	12,0	6	0,8	—	6	—	—	3,0	—
„ N	11,5	9	0,5	—	—	5	—	—	4,0
30.7— 5.8	15	3	7,0	8,5	6,8	5,5	17,0	19,6	11,0
5.8—10.8	18	2	—	8	7,5	5,7	20,0	18,8	14,3
10.8—15.8	14	3,5	1,4	—	8	6	—	11,2	8,4
15.8—25.8	11	12	0,8	—	8,5	6,5	—	6,8	5,2
25.8—30.8	10	> 20	< 0,1	—	8,5	7,5	—	~ 0,5	~ 0,4
30.8— 7.9	6	00	0	—	8,5	7,5	—	—	—
7.9—17.9	4	00	0	—	8,5	—	—	—	—

<div align="center">

Durchschnitt Eier/Gelege   Summa Eier/♀

5,8   6,7   5,3   64,4   66,4   54,9

</div>

geringen Einfluss von Prädatoren unter dieser Zeit, darf man annahmen, dass die grössten Verluste während der Eiphase eintreffen. Da die Eier zu ihrer erfolgreichen Entwicklung höchstwahrscheinlich eine Gefrierperiode benötigen, lässt sich leicht ausdenken, auf welche Weise ein Grossteil von ihnen verloren geht.

Weiter lässt sich ableiten, dass eine Erhöhung des Überlebensprozentsatzes von 2 % auf 4 % eine Verdopplung des nächstjährigen Bestandes bedeutet und umgekehrt eine Verringerung dieses Satzes auf 1 % eine Halbierung. Damit zeichnet sich ein sehr einfacher Regulierungsmechanismus für den *Polyartemia*bestand eines Gewässers ab. Je grösser die Weibchen, desto grösser ihre individuele Eiproduktion und desto grösser der Bestand der nächsten Generation. Ein grösserer Bestand aber führt über Nahrungskonkurrenz zu schlechterem Zuwachs und damit zu geringerer Eiproduktion und schliesslich zur Verringerung der folgenden Generation. Dieser Mechanismus ist keineswegs selbstverständlich. Im Gegenteil führt Nahrungsmangel bei vielen Organismen zu gesteigerter Fertilität und erhöhtem Konkurrenzdruck. Wir haben es also hier mit einer ausgesprochen „modern" wirkenden um nicht zu sagen vorbildlichen Anpassung an die spezielen Gegebenheiten des arktischen Biotops mit seinen begrenzten Lebensbedingungen zu tun.

Der Energiebedarf von *Polyartemia*

Die Nahrung

Untersuchungen des Darminhalts einer Anzahl von Tieren von verschiedenen Probenahmen ergaben folgendes. Der Füllungsgrad des Darmes war am grössten im Överste Tretjärn und klar am geringsten im Mellersta Tretjärn. Gleichzeitig zeigten die Tiere des letzteren die beste Verdauung; im Gegensatz zu Tieren aus den beiden anderen Tümpeln waren hier die Algen im Darminhalt stets leer und aufgebrochen. In Tieren aus den anderen Tümpeln konnten völlig unzerstörte Algen noch im hintersten Teil des Darmes vorkommen, was auf einen schnellen Nahrungsdurchschub deutet.

In Mellersta und Nedre Tretjärn war die Magenfüllung gegen Ende der Periode deutlich geringer. Unterschiede zwischen den Geschlechtern waren keine zu finden. Bei beiden bestand die Nahrung praktisch nur aus benthischen Algen. Wie parallele Zählungen des Phytoplanktons des freien Wassers ergaben, war dieses völlig ohne Bedeutung für die Ernährung der Tiere.

Die wichtigste Rolle spielten grössere und kleinere *Oocystis*-Arten und verschiedene Desmidiaceen wie *Staurastrum*, *Cosmarium* und *Arthrodesmus*, die in diesen Tümpeln sämtlich am Boden leben. Als Subdominanten waren Bodendiatomeen der Gattungen *Pinnularia*, *Frustulia*, *Fragilaria* und *Tabellaria*, Desmidiaceen der Gattungen *Euastrum*, *Xanthidium* und *Hyalotheca*, ferner auch *Oedogonium* und *Botryococcus Braunii* zu verzeichnen. In einzelnen Fällen konnten Rotatorien und Pollen festgestellt werden. Die Kieselalgen hatten nur im Övre Tretjärn klar quantitative Bedeutung für die Ernährung der Tiere. Eine gewisse Succession war in allen drei Tümpeln merkbar. Am Anfang der Untersuchungsperiode dominierte *Oocystis* stark, am Ende Desmidiaceen, grüne Fadenalgen und *Botryococcus*.

Respiration

Um auf indirektem Wege eine grobe Auffassung von Energiverbrauch der *Polyartemia* zu bekommen, wurden mit erwachsenen Männchen und Weibchen Respirationsversuche durchgeführt. Das durchschnittliche Frischgewicht der Weibchen war 8,4 mg/Individum, das der Männchen 5,8 mg, das Trockengewicht 0,4 bzw. 0,3 mg/Individuum oder ca. 5 % des Frischgewichts. Während die Parallelversuche sehr gute Übereinstimmung zeigten war der O_2-Verbrauch besonders bei höheren Temperaturen bei längerer Eponierungszeit merkbar tiefer, nämlich bis zu 40 %. Es ist wahrscheinlich, dass hier bereits Artefakte sich geltend machen, jedoch werden in Tabelle 2 die Mittelwerte aller Versuche wiedergegeben.

Das auffälligste Ergebnis der Versuche ist, dass die grösseren Weibchen nicht mehr Sauerstoff verbrauchen als die Männchen. Bezogen auf das Frisch-

Tabelle 2. Die O_2-Konsumtion von *Polyartemia forcipata* bei verschiedener Temperaturen.

Temperatur °C	µg/Ind · h		µg/mg Frischgewicht · h		µg/mg Trocken-gewicht · h	
	♀	♂	♀	♂	♀	♂
1	8,47	8,84	1,00	1,5	23,21	30,00
8	19,93	21,40	2,37	3,72	54,60	72,54
19	31,17	30,49	3,71	5,30	85,40	103,36

gewicht bzw. das Trockengewicht ist der O_2-Verbrauch der Männchen 50 % bzw. 20 % höher als derjenige der Weibchen. Der Unterschied dürfte darauf beruhen, dass die Männchen wesentlich lebhaftere Schwimmer sind als die Weibchen.

Ein Vergleich unserer Resultate mit dem O_2-Verbrauch anderer Süsswasser-crustaceen kan hier von Interesse sein. In einer kürzlich erschienenen Arbeit (MOSHIRI, CUMMINS & COSTA 1969) wird ein grössenmässig mit *Polyartemia* vergleichbares Planktontier, *Leptodora hyalina* LILLJEBORG, in dieser Hinsicht untersucht. Fig. 7 zeigt, dass die Respirationsleistung beider Organismen etwa in der gleichen Grössenordnung liegt, dass aber unterhalb 10°C *Polyartemia* bedeutend stärker respiriert, während sie oberhalb 20°C eher sparsamer im O_2-Verbrauch ist als *Leptodora*. Letzteres bestätigte sich auch in der Tatsache dass hohe Konzentrationen von *Polyartemia* tagelang in Aquarien mit 25-gradigen Wasser gehalten werden konnten ohne irgend welche Schädigungen zu zeigen. Die relativ hohe Respiration von *Polyartemia* bei niederer Temperatur erklärt sich natürlich aus der Anpassung ihrer physiologischen Funktionen an solche Temperaturen, wo die der Warmwasser-species *Leptodora* bereits gelähmt werden.

Vergleichsbeispiele für kleinere Planktontiere liefern die Resultate von VOLLENWEIDER & RAVERA (1958). Im Bereich von 15°C fallen ihre Werte für *Daphnia obtusa* (KURZ) und *D. Longispina* O.F.M. in die gleiche Grössenordnung wie die von *Leptodora* und *Polyartemia,* während der Copepode *Mixodiaptomus laciniatus* (LILLJEBORG) wesentlich geringeren O_2-Verbrauch zeigt, als die Phyllopoden.

IV. Produktionsberechnungen

Die grösste Schwierigkeit für eine Berechnung der Gesamtproduktion ist das Fehlen quantitativer Ziffern für die *Polyartemia*bestände in den drei Tümpeln. Dass solche im Rahmen eines vernünftigen Arbeitsaufwandes nicht zu gewinnen waren, beruht auf der heterogenen Verteilung der Tiere im Wasser (Seite 63).

ml O$_2$ /mg Trockengewicht · h
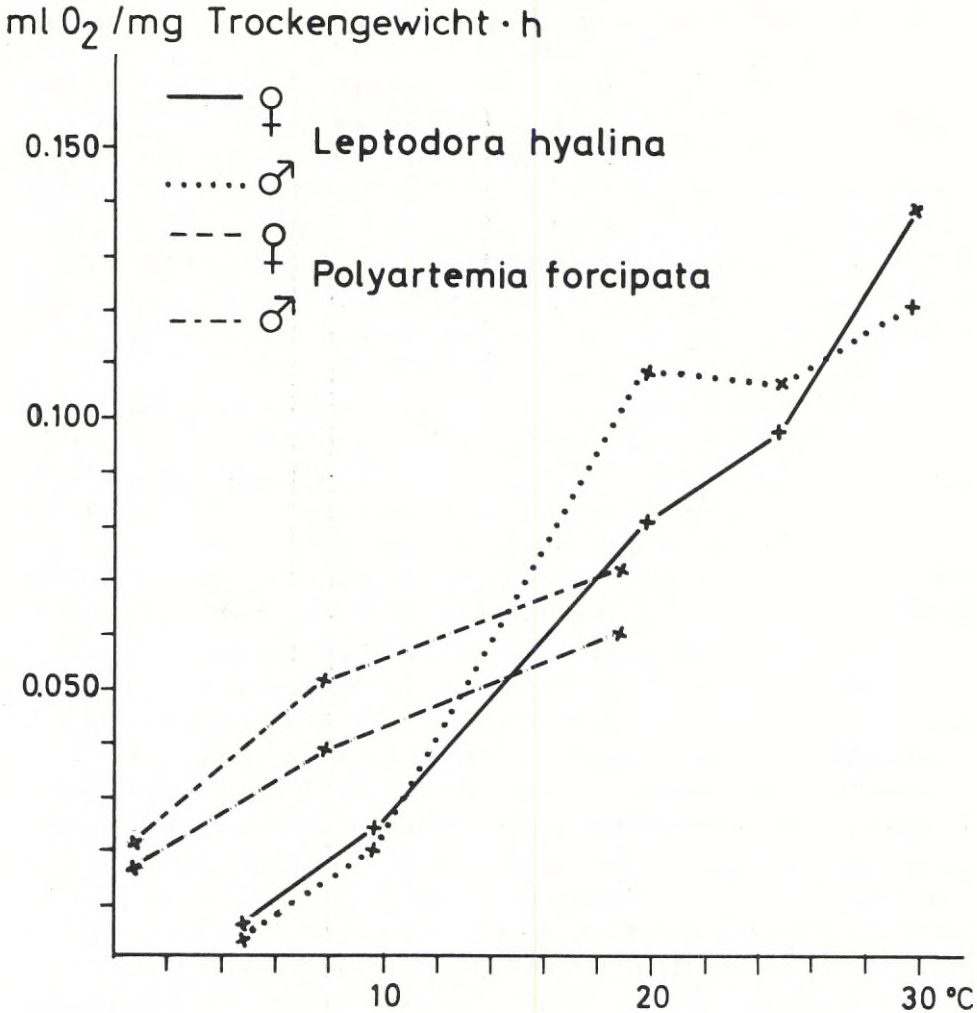
Fig. 7. Der Sauerstoffverbrauch von *Polyartemia forcipata* und von *Leptodora hyalina* in Abhängigkeit von der Temperatur.

Eine Produktionsberechnung auf Individuumsbasis lässt sich indessen anhand der bisher dargelegten Zahlen durchführen. Die Werte sind zu grob, um eine Aufteilung in die verschiedenen Tümpel und in verschiedene Zeitabschnitte zu gestatten, genügen aber zur Behandlung der Produktionsperiode als Ganzes.

Nach Fig. 2 kan die Mitteltemperatur der Produktionsperiode auf 12°C festgelegt werden. Bei dieser Temperatur respirieren adulte Tiere rund 0,6 mg O$_2$/Tag (interpoliert und umgerechnet aus Tab. 2), was einem Gegenwert von ca. 0,2 mg Kohlenstoff entspricht. Leider fehlen Respirationsmessungen

an Larven. Wahrscheinlich respirieren diese relativ stärker als die Adulten, einfachkeitshalber sei aber die Hälfte von deren Werten, d.h. 0,3 mg O_2 bzw. 0,1 mg C angenommen. Die Tiere leben insgesamt etwa 75 Tage (der Övre Tretjärn ungerechnet), davon etwa 15 Tage als Larven (Seite 54—56). Das bedeutet, dass ein Individuum unter seiner Lebenszeit ca. 13,5 mg C verbrennt, davon 1,5 mg währen des Larvenstadiums ($15 \times 0,1 + 60 \times 0,2$).

Das Trockengewicht der adulten Tiere betrug im Mittelwert für Männchen und Weibchen rund 0,35 mg/Individuum (Seite 59). Nach ULÉN (1971) bestehen 50 %, also 0,18 mg davon aus Kohlenstoff. Ungefähr 3/4 seines End-gewichtes erreicht das Tier auf dem Wege vom Ei zum Adulten, der Rest kommt während der restlichen Lebenszeit hinzu.

Die Eiproduktion beträgt mindestens 50 Stück pro Weibchen (Tab. 1). Die Eier haben einen mittleren Durchmesser von 450 μ (Seite 54) oder ein Volumen von gut $40 \cdot 10^6 \mu^3$, was bei einem spezifischen Gewicht von 1 (in Wirklichkeit etwas mehr) 40 μg entspricht. Das Trockengewicht der Eier dürfte bedeutend höher sein als das der Tiere und sei hier als 10 % angesetzt. Bei einem Kohlegehalt von 50 % des Trockengewichtes bedeutet das, dass ein Weibchen im Durchschnitt etwa 0,1 mg C in der Eiproduktion investiert.

Ein Individuum verbraucht, oder genauer gesagt benützt also während seiner Lebenszeit rund 14 mg Kohlenstoff, die Weibchen etwas mehr, die Männchen etwas weniger, davon reichlich 10 % während der Larvalent-wicklung. Der unvergleichbar grösste Teil dieser Menge, nämlich 95—98 % liefert Bewegungsenergie. Jeden Tag verbrennt das Tier ebensoviel Kohlen-stoff für seine Schwimmbewegung wie es in seinem Körper eingebaut enthält.

Um eine grob approximative Auffassung der Totalproduktion zu bekom-men lassen sich aus der Anzahl der Netzzüge, der Netzöffnung und der jeweils durchfischten Strecke die jeweiligen Bestände auf 50 Individuen pro m^3 im Övre Tretjärn, 25 Individuen pro m^3 im Mellersta Tretjärn und 75 Individuen pro m^3 im Nedre Tretjärn abschätzen, was Absolutwerten von einigen zehntausend und kaum mehr als hunderttausend Tiere pro Tümpel entspricht. Setzt man den C-Gehalt von Algen auf 5 % ihres Frischgewichts, 70 ergibt sich ein Nahrungsbedart der *Polyartemia* von mindestens 1—2 g frischer Algen pro Saison und m^2 Tümpelfläche.

V. Übrige Boebachtungen

Abnormitäten

Im untersuchten Material fanden sich drei atypische Tiere, die verschiedene Grade von Übergängen zwischen Männchen und Weibchen darstellten. Zwei von ihnen vereinigten weibliche Hauptmerkmale mit im einen Falle kleinen Frontalbeihängen an der Stirn, im anderen Falle mit geteilten zweiten An-
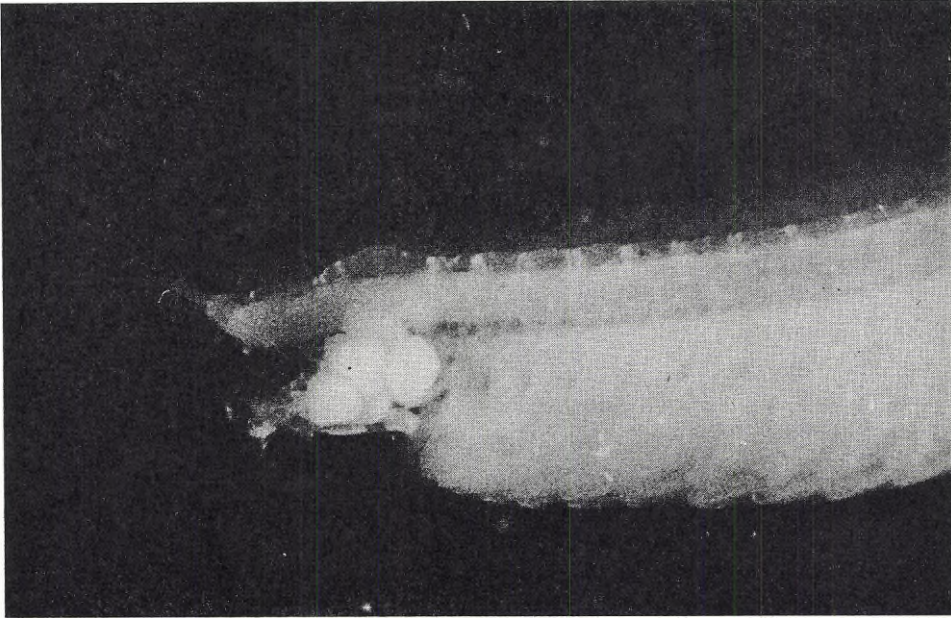
Abb. 2. *Polyartemia forcipata*. Intersex.

tennen. Das dritte Tier (Abb. 2) war ein ausgeprägter Intersex mit der Körperform des Männchens aber mit 6 Eiern im vergrösserten Geschlechts- organ, welches jedoch in keiner Weise der weiblichen Eikapsel entsprach. Ausserdem waren die Antennen dieses Individuums weniger kräftig ausge- bildet als bei normalen Männchen.

Schwarmbildung und Migration

Wie erwähnt, waren Horizontal- und Vertikalverteilung der Tiere im Wasser stark heterogen. Bei klarem und ruhigen Wetter hielten sich die Tiere hauptsächlich im freien Wasser auf, bei Wind und bedecktem Himmel un- mittelbar über dem Boden. Im Aquarium konnte durch gerichtete Beleuchtung jederzeit kräftige Phototaxis provoziert werden. Im offenen Wasser bildeten die Tiere dichte Schwärme, die nach visueller Schätzung Dichten bis zu 10 Individuen pro Liter und Aussmasse von einem halben Kubikmeter erreichen konnten. Besonders gegen Ende der Saison konnten noch grössere Einheiten z.B. längs eines Strandes beobachtet werden und es schien nicht ausgeschlos- sen, dass der gesamte Bestand eines Tümpels in einem solchen Schwarm vereinigt war. Soweit sich die Tiere am Boden aufhielten, wurden steinige Gebiete sichtlich gemieden und weiche bzw. vegetationsbedeckte Sedimente bevorzugt. Die Verteilung der Tiere war in solchen Fällen gleichmässiger.

Polyartemia als Nahrungsobjekt

Ihre langsame und einfache Schwimmweise lässt *Polyartemia* zu einer leichten Beute für grössere Wassertiere werden, weshalb sie auf die Dauer kaum mit solchen zusammen leben kann. Ihre gewöhnlichen Feinde in diesen Tümpeln sind Dytisciden und für jüngere Stadien vielleicht auch gewisse Chironomiden. Das in Abschnitt „Die Lebensdauer der Adulten" erwähnte Beispiel, nach dem im Övre Tretjärn Wasservögel in kurzer Zeit den *Polyartemia*bestand des Tümpels praktisch aufzehren konnten, zeigt indessen, auf welche Art auch „aussenstehende" grössere Predatoren an der Produktion arktischer Kleingewässer teilhaben können. Wie aus der Berechnung der Eiproduktion von *Polyartemia* hervorgeht, verträgt eine Population einen gelegentlichen Aderlass dieser Grössenordnung ohne weiteres. Aber sollte er sich während einer Reihe von Jahren ständig wiederholen, so würde die Existenz der Art im betreffenden Gewässer schnell infrage gestellt. Dies wird bei Gegenwart von Fisch der Fall. KARLSSON & NILSSON (1968) erwähnen ein derartiges Beispiel aus dem See Pieskejaure im Oberlauf des Piteälv. In den zuvor fischfreien See wurden Saibling und Forelle eingesetzt. Nach kurzer Zeit konnte im See keine *Polyartemia* mehr nachgewiesen werden. In einem See im Rovejauregebiet im westlichen Padjelanta dagegen (mündliche Mitt. von G. KJELLBERG) erwies sich *Polyartemia* als dominierender Nahrungsorganismus im Magen von Saibling, ohne dass die Art im See festzustellen gewesen wäre. Offensichtlich waren die Tiere hier aus den reichen Beständen nahegelegener Tümpel ausgespült und von den Fischen an der Einmündung der Bäche abgefangen worden.

VI. Zusammenfassung

In drei alpinen Tümpeln in der Nähe des Sees Latnjajaure in Schwedisch-Lappland wurden vergleichende Studien über Biologie und Populationsdynamik von *Polyartemia forcipata* (FISHER) durchgeführt.

Entwicklungsgeschwindigkeit der Larven, Zuwachsgeschwindigkeit der Adulten sowie Intensität der Eiproduktion sind in erster Linie temperaturabhängig. Die Entwicklung der Larven beginnt bei etwa 4—5°C, die Entwicklung von Eiern kommt unterhalb 9—10°C zum Stillstand.

Kopulation und Eiproduktion finden statt solange die Tiere leben. Die Eier werden in Gelegen abgelegt, deren Grösse der Länge des Weibchens direkt proportional ist. Für jedes Gelege scheint eine neue Befruchtung notwendig. Die Lebenslänge der erwachsenen Tiere ist etwa 2 Monate. Während dieser Zeit produziert ein Weibchen 9—12 Gelege von insgesamt 50—70 Eiern. Ausschliesslich Dauereier werden gebildet.

Die Larven schlüpfen kurz nach Eisbruch und nach 3 bis 4 Wochen sind die Tiere geschlechtsreif. Nach etwa einer weiteren Woche treten die ersten

Eier auf. Nauplienstadien im strikten Sinne kommen nicht vor. Die Entwicklung der Tiere verläuft successiv, wobei einzelne Körperteile sich bei verschiedenen Individuen ungleich schnell entwickeln können. Wenn die Larven etwa 5 mm Länge erreicht haben, beginnt die Geschlechtsdifferenzierung. Bei Eintritt der Geschlechtsreife sind die Männchen etwa 7 mm, die Weibchen etwa 8—9 mm lang. Die erwachsenen Tiere nehmen zeitlebens an Grösse zu und erreichten hier maximal 12,2 mm (Männchen) bzw. 14,3 mm Länge (Weibchen).

Die erreichte Endgrösse der Tiere ist im erster Linie von der Ernährung abhängig. Das Grössenverhältnis Männchen: Weibchen verschiebt sich mit schlechteren Nahrungsverhältnissen zugunsten der Männchen.

Die Nahrung von *Polyartemia forcipata* besteht hauptsächlich aus Algen der bodennahen Schicht. Bisweilen kann auch kleines tierisches Plankton aufgenommen werden. Phytoplankton spielt bei der Ernährung keine Rolle.

Respirationsversuche ergaben einen temperaturabhängigen O_2-Verbrauch, der bezogen auf das Trockengewicht von der gleichen Grössenordnung war, wie bei anderen planktischen Phyllopoden. Die Männchen zeigten etwa 20 % höhere Werte als die Weibchen. Der totale Energiebedarf während der Lebenszeit der Tiere liess sich auf ca. 14 mg Kohlenstoff pro Individuum berechnen. Etwa 95 % dieser Menge wird als Bewegungsenergie verbraucht.

VII. Summary

The biology and population dynamics of *Polyartemia forcipata* (FISCHER) were studied in three alpine tarns close to the Latnjajaure Station in Swedish Lappland.

The development rate of the larvae, the growth rate of the adults and the intensity of egg production are dependant primarily on temperature. The development of the larvae starts at about 4—5°C, the production of eggs stagnates beneath 9—10°C.

Copulation and spawning continue during the whole life-time of the animals. The eggs are produced in batches, where the number is directly proportional to the length of the female. A new fertilization seems to be necessary for every batch of eggs. The life-time of the adults is about two months. Within this period a female produces 9—12 batches with a total of 50—70 eggs. Only resting eggs are produced.

The larvae hatch from the resting eggs shortly after ice-break. 3—4 weeks later the animals have reached maturity and after one more week the first new eggs appear.

No nauplii-stages in the strict sense of the definition are passed by the larvae. The animals develop successively, and some parts of the body may develop at a different rate in single individuals. Sexual differentiation starts

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at about 5 mm length. Maturity is reached in the males at about 7 mm and in the females at about 8—9 mm length. The adult animals continue to grow throughout their lives. In this case they reached 12,2 mm (males) and 14,3 mm (females) as a maximum. The final size of the adults is dependent primarily on the food conditions. Deteriorating food conditions change the size relations between males and females in favour of the males.

The food of *Polyartemia forcipata* consists mainly of bottom-bound algae. Occasionally small zooplankton can be eaten. The phytoplankton has no significance in the food composition.

Respiration experiments showed a temperature dependant O_2-uptake which, related to dry weight, was of the same order of magnitude as in other planktonic phyllopodes, the males showing about 20 % higher relative values than the females. The total energy consumption during the life time of a single animal could be estimated at 14 mg of carbon. About 95 % of this amount was invested in moving energy.

VIII. References

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Acidity and lactate content in the blood of young Atlantic salmon (*Salmo salar* L.) exposed to high pCO₂

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I. Introduction

Second-summer *Salmo salar* tend to take up resting positions on the bottom of stream aquaria (Höglund, 1961; Sprague, 1968). This is the typical behaviour under "control conditions" (see Table 1) of salmon parr kept isolated in the compartments of the constant-flow and alternating-environment test chamber used by Höglund & Härdig (1969). As was demonstrated in the latter study, well-defined carbon-dioxide tensions in the range 5—80 mm Hg are conveniently established by the addition of hydrochloric acid to flowing bicarbonate-rich Uppsala water. At the sudden confrontation with raised pCO₂, distinctive hyperventilation is displayed, combined with body movements. The intensity of activity is correlated to the amount of the pCO₂ increase. After a while, the fish return to their resting positions, even though the pCO₂ is kept at a raised level. With the same technique Höglund & Persson (1971) demonstrated easily reproducible responses among young salmon to equal pH/pCO₂ fluctuations within 40 min between 7.5 and 6.9 pH units and between 5 and 30 mm Hg, which were repeated at regular 40-min or 24-hour intervals.

The present study was undertaken to get a better understanding of the physiological background to the reactions described by Höglund et al. (1969, 1971). Blood samples were taken from fishes exposed variously long to raised pCO₂. The lactate content and pH were analysed. Two carbon-dioxide tensions were used, *viz.* 20 and 30 mm Hg. According to Cross et al. (1969), hypercapnia is certainly developed. This has not been studied *per se*. Assuming an equilibrium between the pCO₂ in the surrounding water and that in the blood passing the gill capillaries (*cf.* Rahn, 1966), the oxygen transport is very likely impaired as a consequence of the "Root effect" (Root, 1931; Black *et al.,* 1966). Along with an increased oxygen demand during the initial agitation, this may cause an accumulation of lactate in the blood (for references, see von Buddenbroek, 1967; Black *et al.,* 1959; Wendt, 1965).

II. Material and methods

Second-summer parr (*Salmo salar*) supplied by the Fishery Board from the breeding plant and salmon hatchery in Älvkarleby were transported to Uppsala and kept in the laboratory in 250-l aquaria in running aerated tap-water. The chemical composition is shown in Table 1.[1] This water was also used as feed-water for the test apparatus and the fish (20—62 g) were pre-acclimated to this medium for at least one month before being used in the experiments. They were fed daily both in Älvkarleby and in Uppsala with Ewos pellets, standard forage, size 4, furnished by AB Astra, Södertälje, Sweden.

Table 1. Chemical characteristics of the supply water to the storage tanks and the test apparatus (the "control conditions" in the tests). The figures are based on several determinations (*cf.* HÖGLUND, 1961, Table 3, p. 33).

Mg^{++} mg/l	Ca^{++} mg/l	pH	HCO_3- mg/l	CO_2 mg/l	Tot. CO_2 mM	pCO_2 mm Hg	O_2 mg/l	Temp. °C
14.6	86.4	7.5—7.6	300—310	14—15	5.3—5.4	5—6	9.9—10.6	8.6—10.2
	95—119							

One fish was placed in each of the two compartments of the test chamber. The fish took up resting positions and behaved on the whole calmly after 2—4 hours. In order to eliminate possible interference from lactic acid on account of the transfer (WENDT, 1965), no experiments were started during the first 24 hours. At the drainage of 1.4 l/min, corresponding to the velocity of flow of about 3.2 cm/min, the actual CO_2 oversaturations in the water passing the fish become constant within 15 minutes. The coincident values of carbon-dioxide tension, oxygen content (ordinary Winkler determination), and temperature were then arrived at in water from the inlet and outlet of the chamber. The pCO_2 was calculated from the pH, bicarbonate alkalinity, and temperature (see HÖGLUND, 1961). Direct measurements of pCO_2 with the aid of an ASTRUP micro-tonometer (Radiometer AMT-1) confirmed the validity of these calculations.

A fish was withdrawn as quickly as possible and stunned with a light blow on the skull. In most cases blood samples were taken by heart puncture with the aid of a syringe provided with a cannula no. 16 or 18 (the dead space was filled with heparin solution). This procedure takes about 15—60 sec altogether. The fish usually survived. Afterwards no difference in growth rate or well-being were observed, as compared with intact animals. It is a disadvantage that uncontrolled low pressure in the syringe may extract gases from the blood sample. If gas bubbles could be detected, the sample was discarded. In some cases blood was drawn with the aid of a heparinized glass capillary from the dorsal aorta after the truncation of the caudal fin. It is discussable which sampling technique is the best one. For the present purpose, heart puncture seemed to cause least disturbance to the fish.

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[1] Mg^{++} and Ca^{++} were analysed by T. Ahl, the Institute of Limnology at this university.
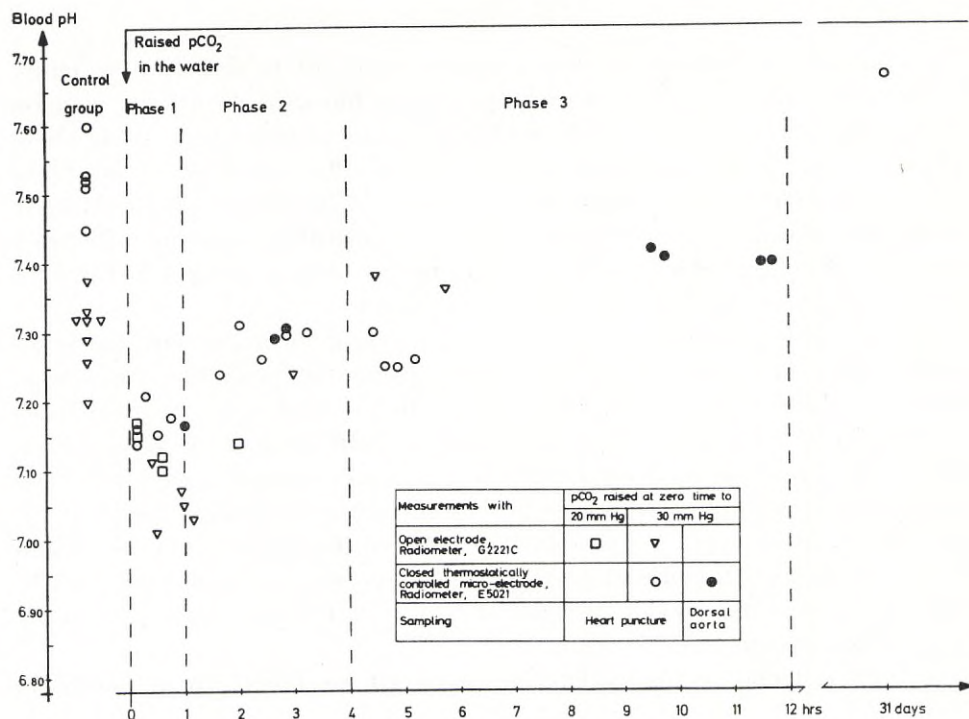
Fig. 1. The pH in the blood of second-summer *Salmo salar* after various exposures to raised environmental pCO_2.

The lactate content was determined in 0.1 ml of blood, according to BARKER & SUMMERSON (1941), modified by STRÖM (1949). The values presented are corrected for the actual heparin dilutions.

Tentative pH measurements were performed on blood samples at room temperature by means of an open glass electrode (Radiometer, G2221C). This electrode could not possibly be filled without bringing the blood sample in contact with the air. The values from these measurements are presented in Fig. 1 and are given without correction for temperature. The remaining pH measurements were made at the actual temperature of the water surrounding the fish. A thermostatically controlled micro-electrode (Radiometer, E5021) was used. In this case the data in Fig. 1 are mostly based on two determinations from each fish. Correction for the heparin dilution in the syringe was not considered necessary (*cf.* ROSENTHAL, 1948).

When sufficient sample volumes were available, the hematocrit was read after the centrifugation of blood in heparinized glass capillaries for 8 min at 5000 g. The original measurements are corrected for the aliquot of heparin.

III. Results

Along with measurements from a control group of 13 fish (water quality as given in Table 1), the changes of pH in the blood of 34 Atlantic salmon parr exposed for varying periods to high pCO_2 are presented in Fig. 1. Three phases of acid-base regulation were discerned. Phase 1 (1 hr; group 1 in Table 2) is characterized by increasing acidity in the blood. The next phase of the test period (3 hrs; group 2 in Table 2) is distinguished by noticeably rising pH. Finally, a third phase was discerned (4—8 hrs; group 3 in Table 2), in which the rise in the blood pH was less rapid.

The pH values measured with the two types of electrodes are not quite comparable. After temperature correction using the procedure for warm-blooded animals due to ROSENTHAL (1948), the pH determinations made with G2221C in the control group almost coincide with those made with E5021. After this correction the average pH for the whole control material is close to 7.50. Temperature correction is less useful in the measurements from the test groups, as steep pCO_2 gradients exist between the samples and the air and because falling pCO_2 and rising temperature have inverse effects upon the pH. The averages of the pH data arrived at with E5021 from phases 1, 2, and 3 were 7.15, 7.30 and 7.35 respectively.[2]

The blood-lactate contents determined on 40 specimens are presented in Table 2.

Table 2. Blood lactate (mg %) from second-summer salmon (*Salmo salar*) after various exposures to raised pCO_2 in the ambient water (see Fig. 1). The water temperature was 8.6—10.2°C. Means are given with the standard error. The test groups are compared with the control group by Student's t-test. The test groups correspond to phases 1—3 in Fig. 1

	Control group	Test group 1 0—1 hr	Test group 2 1—4 hr	Test group 3 4—12 hr
n	10	13	11	6
$\bar{x} \pm \frac{s}{\sqrt{n}}$	9.7± 1.06	15.2± 3.16	11.1± 0.79	10.6± 1.74
Range	3.3—15.2	4.6—40.8	7.5—17.0	5.6—16.0
t	—	1.647	0.549	t_s*=0.410
p	—	< 0.95	< 0.80	< 0.70

* $t_s = t \sqrt{\dfrac{v-2}{v}}$ (v is the number of degrees of freedom); corrected for n < 10 (de WEIR, 1960).

As Table 2 shows, no significant differences in lactate content were found in the fish from groups 1—3, as compared with those in the control group.

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[2] Averaged pH are expressed to the nearest 0.05 pH unit. On averaging pH values, see TURRELL (1946).

The whole data regarding lactate content presented in Table 2 coincide with those given by WENDT (1965) for rested salmon parr of the same age. The slight difference in group 1 is due to two lactate values (40.8 and 34.0 mg %). However, the corresponding blood pHs, 7.10 and 7.13 respectively, are not the most extreme ones within this group.

It is concluded that the transient acidosis observed is not caused by a lactate accumulation. Accordingly the acidosis just seems to depend upon an unbalanced hypercapnia caused by the CO_2 treatment.

The high pCO_2 during the test, as compared with that under the control condition, also gives rise to an increase in haematocrit. This may be due to the swelling of red cells (IRVING et al., 1941) and/or a loss of fluid from the blood (BLACK et al., 1959). With few exceptions no haemolysis was observed. This will be discussed in a later publication.

IV. Discussion

According to CROSS et al. (1969), in Squalus acanthias "observations indicate that acute hypercapnia in a low pCO_2 species is accompanied by a sharp rise in plasma $[HCO_3^-]$". Thus, if the excess of hydrogen ions during the unbalanced phase of hypercapnia (especially phase 1 in Fig. 1) produced in the present type of experiments is buffered or if the protons are excreted, the normalization of pH in the blood observed (Fig. 1) is due to increased $[HCO_3^-]$ in the plasma. The hydration of CO_2 and the dissociation of H_2CO_3 occur rapidly. In the process of removing the acidosis in the state of unbalanced hypercapnia, the neutralization of the excess of protons is apparently the most time-consuming phase.

In Squalus acanthias CROSS et al. (1969) did not observe a sufficient increase in the excretion of H^+ over the gill epithelium or enough titratable acids in the urine to explain the total increase of $[HCO_3^-]$ appearing during hypercapnia in the plasma. Organic bases may be mobilized in the regulation of pH after the initial acidosis. Substances of rather unknown function, like anserine, may take part in this restoration (COWEY et al., 1962). If the increased haematocrit observed is partly due to the swelling of the erythrocytes, this points to the buffering action of haemoglobin.

For the explanation of the present observations, the ideas put forward by CHERNIACK & LONGOBARDO (1970, p. 223) are suggestive: "For example, the active generation of new quantities of buffer by cells exposed to elevated CO_2 tensions would result in an increase in the slope of the tissue CO_2 dissociation curve."

DAHLBERG et al. (1968) showed that the swimming capacity of Oncorhynchus kisutch increased in a water with high carbon-dioxide tension if the fish were pre-acclimated to this medium for about 20 hours: "The importance of the effect of carbon-dioxide on blood and oxygen transport perhaps has

been overemphasized in the past" (p. 67). The observations made in the present study of an effective acid-base regulation in response to environmentally raised pCO_2 is in keeping with these observations.

This regulation must have an effect upon the ventilation pattern and body movements described by HÖGLUND & HÄRDIG (1969). As Table 2 shows, increased lactate content in the blood can be dismissed in the discussion of the control of these activities. The agitated movements of the fish give rise to metabolic CO_2 (see, for example BLACK et al., 1959, Fig. 1). This adds to the amount of CO_2 diffused into the blood from the CO_2 in the ambient water.

For "low pCO_2 species" (CROSS et al. 1969; see above) there are no problems in getting rid of metabolic CO_2 in their natural habitats, where pCO_2 as a rule is low. Without an acid-base-regulating capacity, the CO_2 conditions in the present experiments would probably be detrimental in the long run. Anyhow, the initial unbalanced hypercapnia certainly impairs the respiratory function. Hypoxia probably arises on account of the "Root effect" (cf. IRVING et al., 1941; EDDY & MORGAN, 1969). The viscosity probably increases, judging from the higher haematocrit observed (see also IRVING et al., 1941). Even if the metabolic CO_2 abates when the fish takes up a new resting position, a high carbon-dioxide tension in the blood still exists, depending on that in the ambient water. Nevertheless the pH in the blood starts to increase after about one hour's exposure to high CO_2 tension (Fig. 1). This is necessary if the fish is to survive the actual extreme CO_2 conditions, even though the viscosity is certainly higher than normal. According to EDDY & MORGAN (1969), the "Root effect" also persists to some extent. These authors also found increased amounts of haemoglobin in Salmo gairdneri exposed to a high concentration of environmental CO_2.

The results arrived at in the present study evidently cannot explain all the features of the pattern of ventilation in response to a sudden rise in environmental pCO_2 (HÖGLUND & HÄRDIG, 1969). Curve type 1 in Fig. 9 and curve type 2 in Fig. 10 in the last-mentioned paper may be explained, however, by the combined effects of hypoxia and hypercapnia. Then metabolic CO_2 produced during the first phase of agitated bahaviour during the initial part of a period with high pCO_2 in the water may contribute essentially to the initial peak of the ventilation curve shown in Fig. 9 in the paper by HÖGLUND & HÄRDIG (1969) (see also BLACK et al., 1959, Fig. 1). This suggestion is also supported by the fact that the hyperventilation caused by raised, environmental CO_2 tension is essentially higher if salmon parr are kept freely than if trapped in restricting conditions (HÖGLUND & PERSSON, 1971).

These authors also suggest a repeated CO_2-response test as a mean of studying the persistence of possible impairment or damage of the underlying reflex mechanisms which might have been developed previously when fish were exposed to sublethal concentrations of biologically active agents, for example, those occurring in waste water.

V. Summary

The present study is concerned with the transitory changes of pH and lactate content in the blood of young salmon (*Salmo salar* L.) in response to raised pCO_2 in the ambient water. An effective acid-base regulation was found to counteract a pronounced acidosis induced by a sudden rise of pCO_2 in the ambient water. The acidosis is not correlated to any significant changes of blood lactate.

VI. Acknowledgments

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Effects of locomotor restraint and of anaesthesia with urethane or MS-222 on the reactions of young salmon (*Salmo salar* L.) to environmental fluctuations of pH and carbon dioxide tension

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I. Introduction

The present investigation is a complement to previous studies by HÖGLUND & HÄRDIG (1969). HÖGLUND (1961) showed that young salmon readily assume resting positions on the bottom of a continuous-flow aquarium (see also SPRAGUE, 1968). This is even the case when placed in a test chamber (Fig. 1) and exposed to a flow of aerated Uppsala water to which they have been pre-acclimated (Table 1). Then after some hours the fish display regular ventilation. When the carbon dioxide tension is suddenly raised by an addition of hydrochloric acid to this bicarbonate-rich water, excited swimming and hyperventilation are induced. The intensity of these effects is dependent both on the magnitude and the duration of the change in pCO_2 (HÖGLUND & HÄRDIG, 1969). In the present study several series of experiments were performed, in which freely moving and fixed salmon parr were subjected to identical, repeated variations in the ambient pCO_2 at short (40 min) or long intervals (24 hours). In one series unanaesthetized (intact) parr were tested (Figs. 2 and 3) and in another series parr that had been anaesthetized with urethane or MS-222 before being placed in the test chamber (Figs. 4 and 5). A representative selection of tests performed are presented in Table 4 and Figs. 2, 3, 4, and 5.

The aim was to study the following questions:

(1) The reproducibility of reactions induced by the CO_2 environment. (See Fig. 2 and Tables 2—4.)

(2) The way in which the hyperventilation induced by an increase in the ambient pCO_2 is influenced by simultaneously provoked locomotor activity. (See Fig. 3.)

(3) The way in which previous *immobilization*[1] by urethane or MS-222 anaesthesia affects reflex-controlled reactions to variations in the ambient pCO_2. (See Figs. 4 and 5 and Table 3.)

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[1] By immobilization is meant that the fish is maintained in a bath of anaesthetic solution until no body movements except ventilation are observed. It is then transferred quickly to the test chamber for recovery and the CO_2-response test.
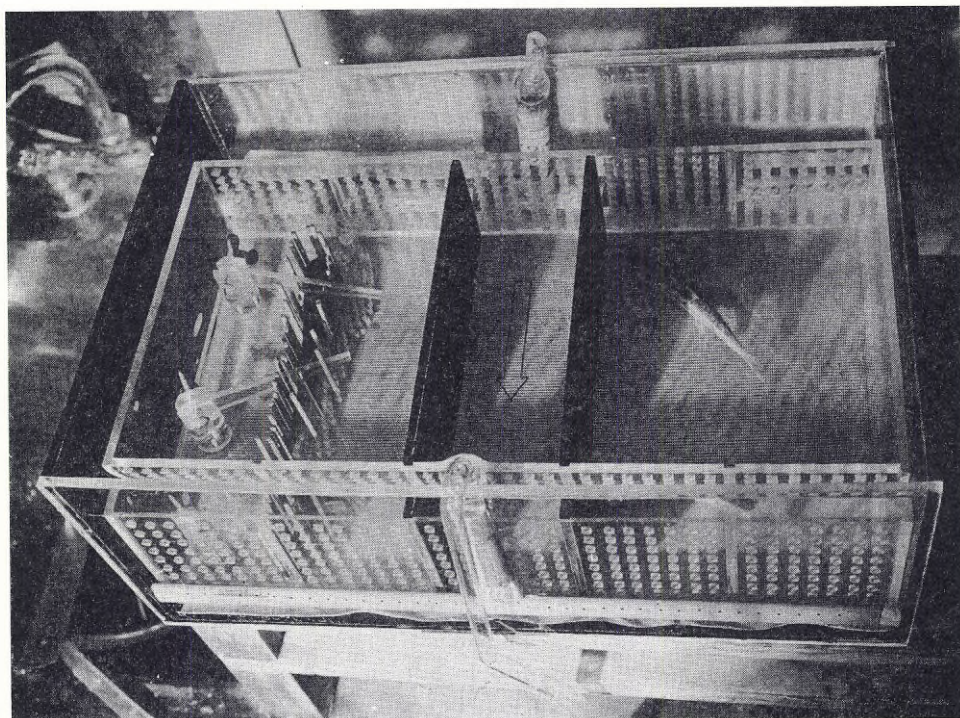
Fig. 1. The constant-flow and alternating-environment test chamber without sheltering hood. Water runs in and out through T-pieces, the cross bars of which contain a number of holes. During the tests the inner comparted box $(10 \times 20 \times 40$ cm) is covered by a glass sheet. A complete sketch is given by Höglund & Härdig (1969, Fig. 2). To the left a fish is tightly fastened in one position on the bottom. The resting position of the other specimen (allowed to swim freely) is typical at a drainage of pure aerated Uppsala water of about 2.5 cm/sec.

II. Fish material and test techniques

The fish were obtained from the Board of Fisheries salmon-breeding plant in Älvkarleby, Sweden. They were hatched in April in the River Dalälven (pH 6.4—6.5; HCO_3^- 8 mg/l; O_2 about 11 mg/l) and were brought to Uppsala in September the following year. The pre-acclimatization aquarium and the test chamber were supplied with water of the same quality (Table 1). Two specimens of fish were placed in the test chamber, one in each of two separate compartments provided with a cover; one fish was allowed to move about freely in the compartment and the other was fixed in one position (left, Fig. 1); moveable pegs, fixed into a floor plate, formed a fence around the fish, which was also restrained above by a polyvinyl chloride tube, which is not shown in Fig. 1. At the time of the tests the fish weighed 15—50 g and measured 12—17 cm. The tests were performed during the winter months, October—February.

Table 1. Chemical characteristics of the supply water to the storage aquaria and test apparatus, based on several samples; these represent the "control conditions" in the test series.[2]

Mg++ mg/l	Ca++ mg/l	pH	HCO$_3^-$ mg/l	CO$_2$ mg/l	Tot. CO$_2$ mM	pCO$_2$ mm Hg	O$_2$ mg/l	Temp. °C	$\varkappa \cdot 10^6$ omhos
14.6	86.4 95—119	7.5—7.6	300—320	14—15	5.3—5.4	5—6	9.9—10.6	8.6—10.2	580

In the experiments during control periods, which are indicated by C and a sequence number, water of the same quality as that in which the fish had been pre-acclimatized was used. The pCO$_2$ was raised and lowered during test periods indicated by T and a number. These changes were produced by adding 0.3 M HCl at 9 ml/min for 20 min, to the feed water flowing at about 1.5 l/min through the test chamber; thus the pH decreased and pCO$_2$ increased progressively in the two compartments in the course of 20 min. On discontinuation of the supply of HCl the pH and pCO$_2$ were progressively restored during the following 20 min (Fig. 3). In the figures the test periods are indicated by the pH curves. Corresponding pCO$_2$ changes may be seen in Fig. 1 in HÖGLUND & HÄRDIG (1969, p. 82). Increasing and decreasing pCO$_2$ values are indicated by narrow and wide cross-hatching, respectively.

III. Observations

The ventilation and locomotor behaviour were observed ocularly. The ventilation rate is presented as a function of time, under different environmental conditions in the test chamber, in the form of ventilation curves (Figs. 2—5). The basic elements in the series of behavioural reactions induced by pCO$_2$ variations in the water are indicated by symbols, which are explained in Table 2 (HÖGLUND & HÄRDIG, 1969, Table 4, p. 94). During the period in the test chamber, an erratic behaviour was also observed on some occasions, and this is indicated by "P" (see Fig. 4).

During anaesthesia with urethane or MS-222, partly different reactions were noted. For these, the symbols explained in Table 3 have been used (cf. MARCHETTI 1962, Fig. 55, p. 176).

IV. Experiments with unanaesthetized salmon parr

A. Results

The following section concerns the reproducibility of the reactions and the relation of the ventilatory response to the type of locomotor and body movement behaviour in free and fixed salmon parr.

[2] According to analyses performed by T. AHL, the Institute of Limnology, University of Uppsala. Cf. also HÖGLUND (1961, Table 3, p. 33).
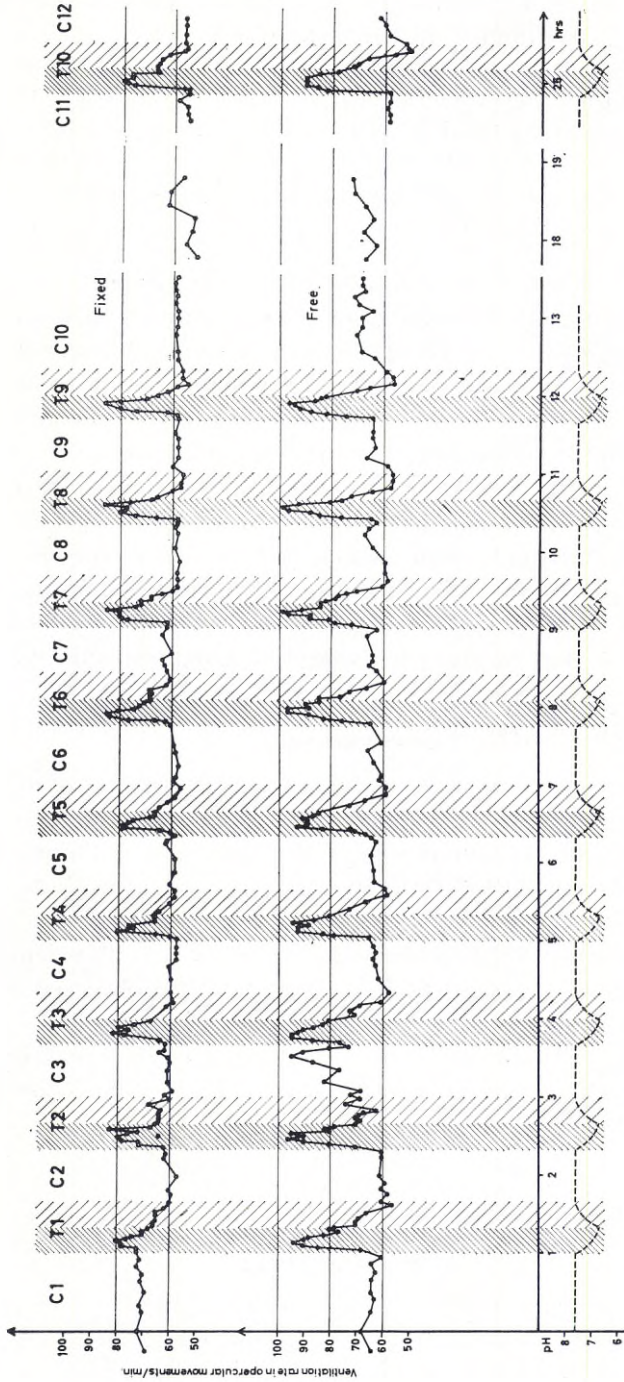
Fig. 2. The ventilatory pattern of two Atlantic salmon parr which were exposed repeatedly (T1, T2, . . T10) to identical changes of pH and pCO₂ in well bicarbonate-buffered water (see lower curve of short dashes, Table 1, and Fig. 3). One fish was fastened tightly and the other was free, as shown in Fig. 1. Both behaved calmly during the periods C1, C2, . . . C12 when pure aerated Uppsala water was drained through the test chamber. When confronted with increasing pCO₂ in the environment (areas of narrow, cross-hatching in the diagram, T1, T2, . . . T10) they became excited. This is manifested by increasing ventilation as well as agitated behaviour (see Table 4).

Table 2. Symbols used for the elements of behavioural changes provoked by increases in pCO_2 obtained by the addition of hydrochloric acid to running bicarbonate-rich, aerated Uppsala water.

Phase no. in time sequence	Behaviour of a fixed salmon parr	Symbol		Behaviour of a salmon parr moving freely in the test compartment
1	The fish is largely inactive	o	o	The fish is largely inactive in a resting position on the bottom. No distinct fin movements
2	The fish displays clear movements, mainly with the pectoral fins	O	O	The fish lies at the bottom and shows clear movements with the pectoral fins
3	The fish makes strong fluttering movements as if in an attempt to free itself from the restraining device	K	Z	The fish swims around in the compartment
4			Y	The fish is seen mainly immediately beneath the lid of the test compartment

Fig. 2 and Table 4 show the reactions in a free (25 g; 16 cm, lower curve in Fig. 2) and a fixed fish (26 g; 14 cm) during 10 identical test periods. The changes in pH and pCO_2 during each of these 40-min periods (T1—T10 in Fig. 2) are illustrated graphically in Fig. 3. The ventilation curves in this figure are plotted on the basis of the mean values from T1—T9 in Fig. 2; unfilled circles represent the fixed salmon parr and filled circles those that were allowed to move freely. During the periods T1—T10 both the free and fixed parr exhibited well reproducible reactions concerning ventilation and locomotor behaviour.

In another experiment two salmon parr were maintained in the test chamber without food for 51 days (see Fig. 1). During this time they were tested 24 times as shown in Fig. 3. The intervals between the test periods were

Table 3. Symbols used to describe the behaviour of salmon parr during exposure to urethane or MS-222 solution.

Phase no.	Behaviour	Symbol
1	After being placed in the bath of anaesthetic solution the fish assumes a resting position on the bottom or swims around relatively calmly.	s
2	The fish lies immobile at the bottom in a lateral position and shown clear ventilatory movements.	S
—	The degree of uprightness, normal body position, abdomen uppermost, imbalance, are indicated by arrows, the tips of which show the position of the dorsal fin.	↓↑→etc.

at least 24 hours. CO_2-induced reactions corresponding to those shown in Fig. 3 and Table 4 were recorded. There was no appreciable difference in these reactions even though the general condition of the fish may have deteriorated.

The freely moving parr in Fig. 2 began to hyperventilate simultaneously with movement of its fins (symbol O in Table 2). Immediately afterwards it began to swim upwards (symbol Z), and climax of active swimming around the compartment was reached when the ventilation rate was at its highest (symbol Y). The locomotion then decreased in intensity, and after about 20 min the fish again assumed a resting position on the bottom of the compartment (symbol o). This resting behaviour was predominant during the phase of restoration in the control periods. A similar series of reactions was displayed by the fixed parr. Instead of swimming, this fish made fluttering movements within the fixation device (symbol K).

The maximal ventilation rates in the two fish were attained approximately at the same time (Fig. 3). These were reached before the maximal pCO_2 value (about 30 mm Hg) in the ambient water was obtained. The fish whose movements were restrained appeared to show a lower maximal ventilation rate than that which was allowed to move freely. After the maximum had been reached, when the ventilation rate again decreased, a distinct "hump" was seen at several of the curve peaks (Fig. 3). These "humps" appeared to lie at a lower ventilation level in the fixed than in the free parr. Transient hypoventilation occurred at the end of some test periods, especially in those cases when the fish was moving freely.

B. Discussion

HÖGLUND & HÄRDIG (1969) have discussed what mechanisms may possibly control the reactions studied here (*op.cit.*, p. 100):

"The immediate response provoked by an external change of pH/pCO_2 to unnaturally high CO_2 tensions can be regarded as a measure of the *exogenous stress* caused by the abiotic environment. This is most pronounced at the confrontation with the new water quality and shortly afterwards. It implies a *respiratory distress* caused by CO_2 supersaturation in the respiratory medium, either directly by the stimulation of exterior receptors and/or by the action of CO_2 within the animal after a rapid diffusion into the bloodstream and before a new acid-base equilibrium is obtained to re-establish the normal blood pH. This may occur by the retention of blood bases and/or some other *compensatory mechanism, e.g.* the conversion of CO_2 to bicarbonate."

See also *op.cit.*, p. 109 ff., and EDDY & MORGAN (1969).

The possible change in the pH of the blood, suggested in the above citation, is discussed in more detail by HÖGLUND & BÖRJESON (1971), who observed
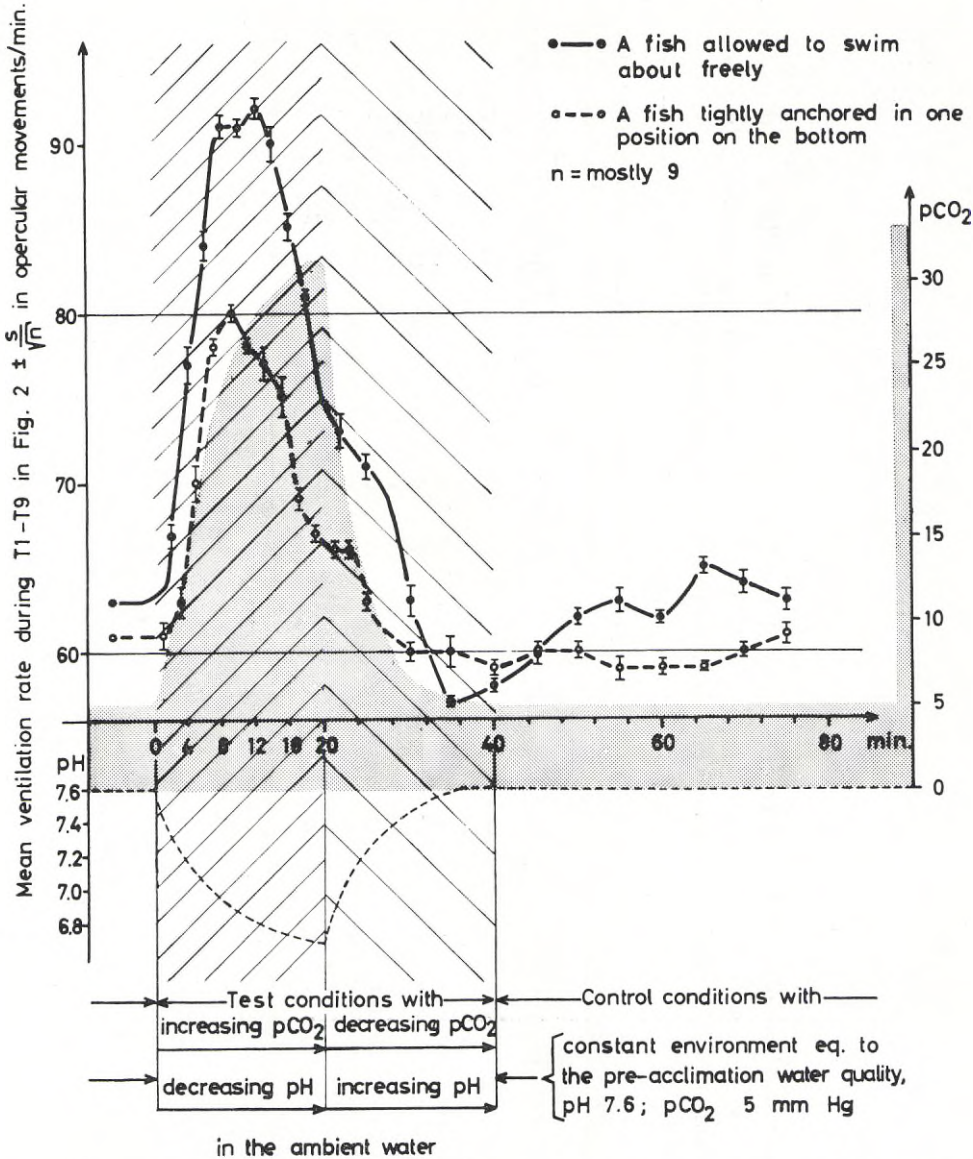
Fig. 3. The "mean hyperventilatory pattern" of the free (continuous curve) and the fixed parr (heavy dashed curve) at the changes of pH and pCO$_2$ chosen (see lower curve of short dashes and shaded area). Open and filled rings are the means of the records of ventilation rates given in Fig. 2 at corresponding phases of pH and pCO$_2$ alterations during T1—T9.

a transient acidosis, not due to accumulation of lactate, in salmon parr at a corresponding age after a sudden elevation of pCO$_2$ in the respiratory medium.

It is reasoned that the ventilation is regulated by the pCO$_2$ in the blood

Table 4. Summary of the behaviour observed in different stages of the test periods T1—T9 in Fig. 2, and the predominant behaviour of two salmon parr, tested simultaneously, in different phases of the change in pCO_2. The symbols are explained in Table 2. The time is given from the start of addition of HCl.

pCO_2 in the water flowing past the fish	Time in min	Salmon parr fixed at the bottom as in the left compartment, Fig. 1									Predominant behaviour	Time in min	Salmon parr allowed to move freely within its compartment (right, Fig. 1)									Predominant behaviour
		T1	T2	T3	T4	T5	T6	T7	T8	T9			T1	T2	T3	T4	T5	T6	T7	T8	T9	
Increasing from about 5 to about 30 mm Hg	1	o	o	o	o	o	o	—	oO	o	o	—	—	—	—	—	—	—	—	—	—	—
	3	o	o	o	o	o	o	o	oO	o	o	2	o	o	o	o	o	o	o	o	o	o
	5	o	o	oO	oO	oO	o	O	o	o	oO	4	O	O	O	o	o	o	o	o	o	oZ
	7	o	o	o	OK	oO	—	—	oO	o	oO	6	Z	OZ	o	O	oO	o	O	oO	o	OZY
	9	o	o	oO	o	o	—		oO	oO	oO	8	ZY	ZY	oO	OZ	o	o	OZ	O	oO	OZY
	11	o	o	o	K	oO	—	O	o	oO	oO	10	ZY	ZY	o	ZY	o	OZ	OZ	OZ	O	OZY
	13	K	K	K	oO	oO	K	O	K	o	oOK	12	Z	ZY	ZO	OZ	ZY	OZ	ZY	OZ	oO	OZY
	15	K	K	K	K	o	—	—	K	K	K	14	ZY	OZ	OZ	OZ	OZ	ZY	Z	OZ	OZ	OZY
	17	K	o	—	o	o	—	—	o	oO	oOK	16	Z	OZ	OZ	OZ	OZ	ZY	N	OZ	OZ	OZ
	19	o	o	oO	K	o	—	—	oO	oO	oO	18	OZ	OZ	OZ	OZ	OZ	O	O	O	OZ	OZ
Decreasing to about 5	21	o	o	—	—	o	—	—	o	o	o	22	o	o	o	o	o	o	o	o	o	o
	30	o	o	o	o	o	—	o	o	o	o	30	o	o	o	o	o	o	o	o	o	o

as long as the pCO_2 in the external medium rises without reaching narcotic values (*e.g.* GUYTON 1966, Fig. 476, p. 596), and that it is also regulated by the pH of the blood. If the possibility of direct CO_2 awareness by hypothetical CO_2 receptors in the gill region is disregarded (KONISHI *et al.*, 1969), then according to the hypothesis the increase in ventilation before attainment of the maximum will be due to the sum of stimulatory action of inwardly diffused CO_2 and metabolic CO_2 and the stimulatory effect of reduction of the blood pH. The ventilation reaches its maximum at approximately the same time as the body movements are most intense (*cf.* Fig. 3 and Table 3). The subsequent decrease in ventilation rate may be due to (1) incipient CO_2 narcosis when a high pCO_2 is accompanied by a low blood pH, or (2) a decrease in the supply of endogenous CO_2 on decreased muscular activity, at the same time as pH in the blood begins to return to normal.

The "hump" in Fig. 3, mentioned above, probably reflects an incipient regulation of the blood pH towards a normal value (HÖGLUND & HÄRDIG 1969, Figs. 3, 4 and 9, and HÖGLUND & BÖRJESON 1971). The subsequent further decrease in the ventilation rate, as well as the tendency to hypoventilation at the end of the test periods, is due mainly to reduced CO_2 stimulation on diminution of the exogenous pCO_2.

The stimulating effect of a sudden elevation of pCO_2 in the respiratory medium may be assumed to be the same regardless of whether the fish is allowed to move freely or is fixed in one position. Added to the carbon dioxide diffused into the blood from the medium, there is probably some supply of endogenous CO_2 arising from muscular metabolism during the initial excitation stage. The difference in hyperventilation pattern in a freely swimming and a fixed salmon parr, which in other experiments was found to be the same as the difference if one and the same fish was allowed free or was fixed, may be due to quantitative disparities in the two forms of movement (swimming and fluttering). It must be remembered, however, that a free fish has a possibility of seeking those parts of the test chamber that are reached somewhat later by water with a higher pCO_2 (HÖGLUND, 1961). The lower maximal ventilation rate in the fixed parr may possibly be due to previous overstimulation by CO_2. Supporting this interpretation is the fact that the ventilatory maximum was reached relatively early, about 10 min after commencement of HCl addition, *i.e.* approximately the same time as the mobile excitation became more pronounced (Table 4). The more rapid increase in ventilation rate in the freely moving fish (Fig. 3) may be due to the fact that added to the stimulatory effect of the CO_2 in and from the outer medium on the ventilation, is the effect of acid metabolites, mainly endogenous CO_2, which is probably accumulated in large quantities when the fish moves about freely. A clearly narcotic effect of endogenous CO_2 was observed in the study by HÖGLUND & HÄRDIG (*op.cit.*), but only at higher carbon dioxide tensions than those of the present study. From the findings of HÖGLUND & BÖRJESON

(*op.cit.*) it would seem that an accumulation of lactate in the blood can be excluded. The amount of movement, the energy conditions and the blood flow may differ in actual swimming, which demands more dynamic muscular work, from those in fluttering movements within the fixation device, where the muscular work is more restricted.

In other words, the alkali reserve is probably influenced in different ways on the addition of different amounts of metabolic CO_2 (*cf.* BLACK, 1958, Fig. 1) in the two forms of exertion. This motivates further studies with thorough blood gas analyses.

V. Effects of previous anaesthesia with urethane or MS-222 on the CO_2 response

A. Background and method

A close study of the ecological, ethological and physiological effects of different toxic substances on various organisms is of value, not least from the aspect of environmental conservation. We will describe here some model experiments in which the effects of exposure to sublethal concentrations of two common fish anaesthetic agents, urethane and MS-222, on the pattern of reaction induced by the pH and pCO_2 environment in salmon parr were studied. These substances were used also with the aim of producing im-mobilization.

Urethane, $H_2NCO_2C_2H_5$, suppresses certain enzyme activities in the carrier chain (JÖBSIS, 1964, p. 89) and inhibits the cholinesterase activity (WEBB, 1967, p. 758). MS-222 (tricaine, propoxate), the methane sulphonate of the ethyl ester of meta-amino-benzoic acid, $H_2NC_6H_4CO_2C_2H_5 + CH_3SO_3H$, is re-commended generally for anaesthetizing fish (*e.g.* BELL, 1967). These anae-sthetic agents have certain similarities in their chemical structure. With re-gard to their anaesthetic effects, reference may be made to BALL & COWEN (1959) and HEALEY (1964).

Screening tests were performed in order to establish suitable conditions under which salmon parr are immobilized but are still able to breathe. Salmon parr were placed in open tanks containing anaesthetic agent dissolved in about 4 litres of stagnant Uppsala water with the same oxygen content and temperature as in the storage aquarium. From here, two fish were quickly transferred to the test chamber where they were allowed to move freely, each in its respective compartment, in a continuous flow of aerated Uppsala water (Table 1). The period in the anaesthetic bath is designated F, with a sequence number, and the period of recovery in the test chamber is designated C. In some cases the salmon parr were tested concerning the CO_2-induced reactions as shown in Figs. 4 and 5. These CO_2 tests were the same as in the experi-ments described in the foregoing section (*cf.* Figs. 2 and 3).

Fig. 4. Ventilation rate and (locomotor) behaviour of three salmon parr during a period in a static bath containing 0.6 % urethane (F9 and F1). When immobilized they were rapidly transferred to the test chamber and kept unrestrained. During recovery one fish stayed in aerated water (C9). The other two (T1, C2, T2 and C3) were exposed twice (T1 and T2) to pH/pCO_2 alterations equal to those in Figs. 2 and 3. One fish exhibited a nearly "normal" CO_2 response after about 6 hours' recovery. For explanation of symbols see Tables 2 and 3.

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B. Results after exposure to urethane

In screening tests with different durations in and concentrations of urethane, the salmon parr showed large individual differences in sensitivity to this form of anaesthesia. The urethane treatment produced a ventilatory disturbance (hyperventilation) which persisted long after the transfer to pure water in the test chamber (Fig. 4, upper recording). The lower recording in Fig. 4 shows the ventilation and locomotor behaviour of two salmon parr (32 g, 15 cm and 28 g, 14 cm) which, after exposure to 0.6 % urethane for 22 min, were transferred to their respective compartments of the test chamber and subjected twice to pH and pCO_2 variations of the same kind as in Fig. 3.

The urethane anaesthesia persisted for a time after the fish had been removed from the urethane solution, but the anaesthetic effect was clearly reversible. This was evident from the fact that after about 7 hours' recovery the CO_2 response in one of the salmon parr was essentially the same as in unanaesthetized parr (*cf.* Fig. 4 with Figs. 2 and 3).

C. Results after exposure to MS—222

From screening tests with MS-222 it was found that a short period of exposure to sublethal concentrations of this anaesthetic produced considerable hyperventilation (*cf.* also RANDALL, 1962), which, in those cases where the fish were immobilized, rapidly regressed when contact with the MS-222 was terminated (F2 and C2 in Fig. 5). The ventilation rate in the anaesthetic bath was considerably higher than at every tolerable pCO_2 increase in aerated Uppsala water (HÖGLUND & HÄRDIG, 1969). The two ventilation curves in Fig. 5 show good agreement during the periods of anaesthesia — 2 hours in 50 ppm MS-222. The lower diagram in Fig. 5 also shows one of five concordant results of CO_2 response tests after MS-222 anaesthesia. After removal of the parr from the MS-222 and transferring it immediately to the test chamber, it is seen that the CO_2 response was at first completely absent. After less than 2 hours' recovery a CO_2 response was again observed (hyperventilatory reaction), of the same typical form as in intact salmon parr (*cf.* Fig. 5 with Fig. 2). The MS-222 anaesthesia had a longer effect on the reaction pattern induced by the CO_2 environment than might have been supposed from the rapid normalization of ventilation in pure, aerated Uppsala water (see upper diagram in Fig. 5). It is more difficult, on the other hand, to trace a corresponding delay by studying the locomotor behaviour, partly because the salmon parr, after recovering consciousness from the MS-222 anaesthesia, again and again displayed anxiety reactions. This behaviour resembles that induced by a sudden increase in pCO_2 in the water (see behaviour symbols in upper diagram in Fig. 5 after 3—4 hours).
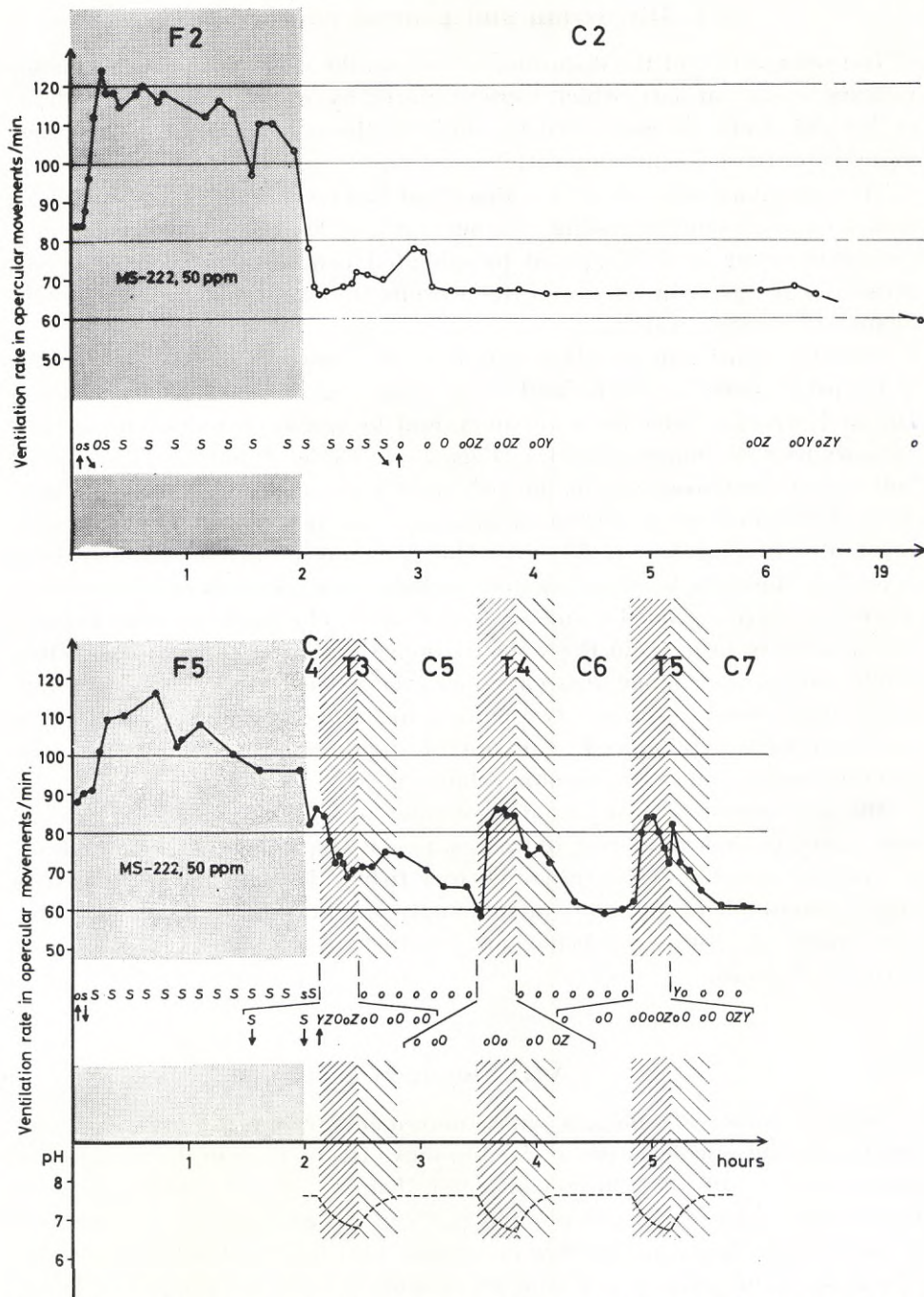
Fig. 5. Two salmon parr exposed for 2 hours to 50 ppm MS-222 (F2 and F5) were rapidly transferred to the test chamber. One was kept in pure aerated water (C2). The other was exposed repeatedly to varying pH and pCO₂ (C4, T3, C5, T4, C6, T5 and C7) in the same way as shown in Figs. 2 and 3. The fish were unrestrained and a "normal" CO_2 response occurred within 2 hours. For explanation of symbols see Tables 2 and 3.

VI. Discussion and general conclusion

The reversibility of the disturbing effects on the ventilatory and locomotor reflexes in salmon parr, which were produced by anaesthesia with urethane or MS-222, could be elucidated by studying the normalization of reactions induced by the CO_2 environment.

The experimental arrangement described in Figs. 4 and 5 may serve as a model for a method of testing whether more or less irreversible reflex disturbances occur in fish exposed to sublethal concentrations of toxic substances or drugs, with effects on the nervous (reflex) function, which might be present in waste water.

In well aerated and bicarbonate-rich water (Table 1) repeated variations of the pH between 7.5 and 6.8 and of pCO_2 between about 5 and about 30 mm Hg gave well reproducible ventilatory and locomotor reactions in second-summer parr of *Salmo salar* (L.) (Figs. 2—5, Tables 2 and 4). This applied both when the movements of the fish were restrained and when they were allowed free movement, within small compartments of a test chamber with constantly flowing water (Fig. 1). The reactions occurred regularly both when the intervals between the test periods were as short as 40 min and when they were extended to one or several days. The reactions were induced by an increase in pCO_2 in the water (HÖGLUND, 1961; HÖGLUND & HÄRDIG, 1969) and did not change their character even when intact salmon parr were kept without food for almost two months in the test chamber. The intensity of the ambient-CO_2-induced ventilatory response was partly related to the simultaneously induced locomotor behaviour.

The technique described should be of value for checking the effect of toxic substances, of topical interest, in waste water. By repeated CO_2-response tests, it might be possible to determine whether fish which have been exposed to certain environmental poisons in sublethal concentrations subsequently display transient reflex- and behavioural disturbances or damage of a more permanent nature.

VII. Summary

Second-summer salmon parr whose movements were restrained were compared with those which were allowed to move freely, each in their respective compartments ($10 \times 15 \times 20$ cm) of a test chamber (Fig. 1), with respect to their response to changes of pH and pCO_2 in the ambient water. Both fish remained calm in a constant flow of aerated, bicarbonate-rich Uppsala water (Table 1). Short periods (40 min) of identical pH/pCO_2 variations (pH between 7.5 and 6.8 and pCO_2 between 5 and 30 mm Hg), which were repeated at regular intervals (40 min or 24 hours), induced well reproducible body movements — fluttering movements within the restraining device in the first

case and excited swimming in the second — and hyperventilation (Tables 2—4, Fig. 2). The maximal ventilation during a CO_2 test period was higher in the fish that was allowed to swim (Fig. 3). The importance for the ventilation rate of variations in the ambient carbon dioxide tension and of an assumed difference in accumulation of endogenous carbon dioxide with the different types of movements is discussed. The degree and duration of reflex disturbances induced by urethane or MS-222 were studied in unrestrained fish by repeated CO_2-response tests (Figs. 4 and 5).

VIII. Acknowledgment

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Characteristics of two discrete populations of Arctic char (*Salvelinus alpinus* L.) in a north Swedish lake

By Nils-Arvid Nilsson and Olof Filipsson

I. Introduction

Scandinavian fishermen and biologists have long known that in many lakes containing arctic char the populations seem to be split up into two or more subpopulations, characterized by different size, coloration, spawning habits, habitat selection, etc. As early as 1832 the Swedish zoologist Sven Nilsson attempted to distinguish the different forms scientifically. He described no fewer than six species, namely *Salmo alpinus* L., *S. salvelinus* L., *S. pallidus* Nilsson, *S. ventricosus* Nilsson, *S. carbonarius* Ström and *S. rutilus* Nilsson. Later on (1855), however, he decided to regard the different forms only as "varieties, different forms and colours, resulting from the influence of different waters where they have lived and perhaps the different food items they have enjoyed".[1] So did also many of his followers, *e.g.* Smitt (1886) and Lilljeborg (1891). Smitt distinguished six varieties and Lilljeborg three. This view was maintained by biologists for many decades, although the importance of the phenomenon that two or more separate populations of char could live side by side in the same lake without apparent intermingling was realized by many of them (*cf.* Nyström 1863, Widegren 1863, Trybom 1883, Collett 1879, Ekman 1912).

Later, age analysis revealed strictly different growth rates of the subpopulations (*cf.* Runnström unp. and Olofsson 1932 quoted by Nilsson 1955, Nordeng 1961, Aass 1968 and Klemetsen and Østbye 1967). In several cases habitat as well as time segregation during spawning was noted, and it was observed that the forms used different food niches (Nilsson 1955). Svärdson (1958, 1961) assumed that these populations (sibling species) had invaded the lakes from the Ancylus Lake. He listed 17 Scandinavian lakes with "double" or "threefold" populations of arctic char and concluded (1961): "The species name *alpinus* includes the whole complex of probably three species. Which of them is the real *alpinus*, and what should be the names of the two others, are matters that have not yet been made clear by science".[1]

Scandinavian experiences are very much in agreement with what has been found in other parts of the Palaearctic. Berg (1948) recognized 11 species of arctic char from Russia, Jordan *et al.* (1930) distinguished 4 species from

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[1] Authors' translation.

North America. McPhail (1961) suggests "at least two distinct forms of both *S. malma* and *S. alpinus* in North America". In Iceland as well as in Central Europe similar sympatric populations of arctic char have been described (Neresheimer 1924, Fridriksson 1939, Lamby 1942, Schindler 1950), and Frost's well-known investigations of the Windermere chars (1963, 1965) proved that the different populations of that lake must be regarded as good species.

The present investigation was originally aimed at studying the effects of the invasion of whitefish (*Coregonus sp.*) into a lake containing only arctic char and brown trout. During the course of the investigation it was discovered that there were two populations of char with different growth rates and different shapes of the otoliths (Filipsson 1967), and special attention has therefore been devoted to that problem during the last few years.

The lake, Övre Björkvattnet, is situated in southern Swedish Lappland, at about lat. 65°5 N. Surface area 26.0 km². The only fish species of the lake were arctic char and brown trout (*Salmo trutta* L). until 1963, when whitefish (*Coregonus sp.*) invaded the lake through the damming of a lake situated below Övre Björkvattnet. The existence of two forms of char in Övre Björkvattnet has long been recognized by the local population, who distinguished between the ordinary char ("röding") and the rarer small, littoral char called "blattjen". In the following description the two populations will be referred to as "ordinary char" and "blattjen".

II. Material and methods

The present investigation represents the analysis of 2,069 char over a period of six years as to habitat, food habits, growth rate and spawning characteristics, gillraker and pyloric caeca counts, otolith shape and flesh coloration.

The fish were caught with sets of 9 floated and 18 sinking gill nets with a standardized series of mesh sizes and applied at fixed stations within the lake. The fish were removed from the floated nets twice: one in the morning and again in the evening. From the sinking nets they were removed only in the morning. The floated nets were moved vertically by stages every second day in such a way as to fish from the surface down to 60 metres. The catch depth of every fish was recorded.

The gillrakers were counted at the first left arch and the pyloric caeca were counted after having been cut away from the rest of the stomach.

The flesh coloration was estimated by a subjective method whereby colour was classified in the field simply as being "white", "slightly pink", "pink" or "red."

The food habits of the fish were analysed by means of a volumetric method

described by NILSSON (1955), and the age was determined by means of oto-liths as described by NORDENG (1961).

Special fishing was carried out during spawning time in order to locate spawning sites and to estimate time of spawning.

Special investigations concerning serum-protein genetics (NYMAN MS) and accumulation of fall-out ^{137}Cs (HANNERZ 1968) were carried out in connection with the present investigation.

III. Taxonomic characters

FILIPSSON's (1967) discovery that it is possible to recognize the two popul-ations of char in Övre Björkvattnet by the shape of the otoliths and the growth rate made it possible to sort out individuals to test whether other taxonomic differences existed.

Otolith shape

Fig. 1 shows the shape of otoliths taken from "ordinary char" and "blatt-jen" in Övre Björkvattnet. Although there is a considerable variation and overlap in the shape of the two types we feel that the following characteristics are valid:

The otoliths of the "ordinary char "typically have their apical end extended to narrow points; the basal lobes also often protrude at more or less sharp angles. The lateral side of the otolith (the side that makes age determination possible) is relatively flat. On the whole the otolith of the "ordinary char" — as compared with the "blattjen" — could be described as "arrowshaped".

The otoliths of the "blattjen" typically have more rounded apical ends, and the basal end is also rounded, without sharply protruding lobes. The lateral side of the otolith is rounded so as to be more or less dome-shaped. On the whole this type of otolith could be described as "drop-shaped".

In young fish it is often very difficult to recognize the two types, and a few intermediate types of otoliths have been found. Further investigations may reveal whether the different shapes merely reflect differences in growth rate, or have a more stable genetical basis.

Gillrakers

The number of gillrakers in char increases as the fish grow to 100—120 mm and remains stable above that size (*cf.* e.g. RESHETNIKOV 1961). The material from Övre Björkvattnet (Fig. 2), however, including specimens ranging from 100 to 230 mm, provides evidence for a slight increase in numbers also above 120 mm. The number of gillrakers of the "ordinary char"
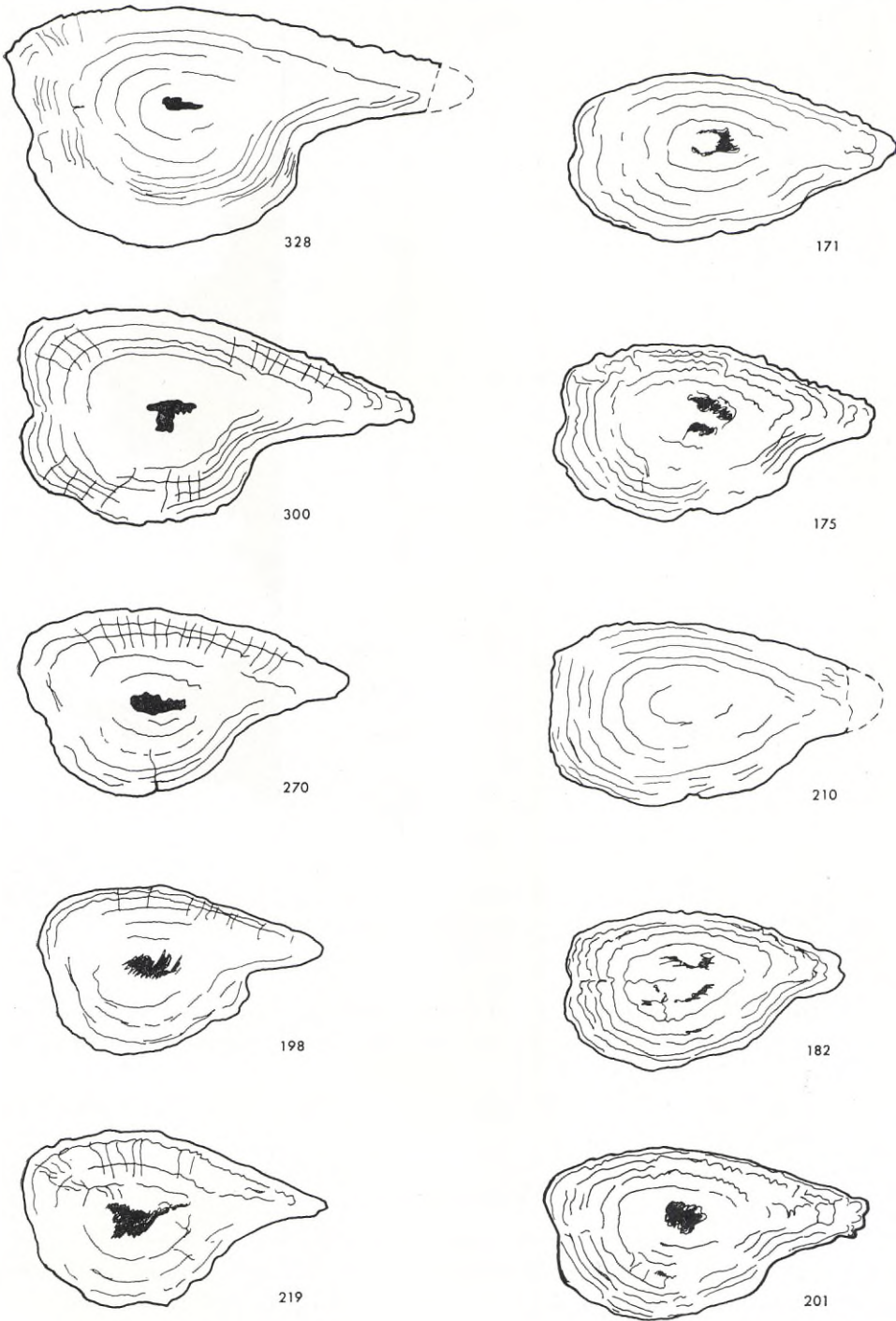
Fig. 1. Otolith shape of "ordinary char" (left) and "blattjen" (right). Numbers represent total length of the fish.
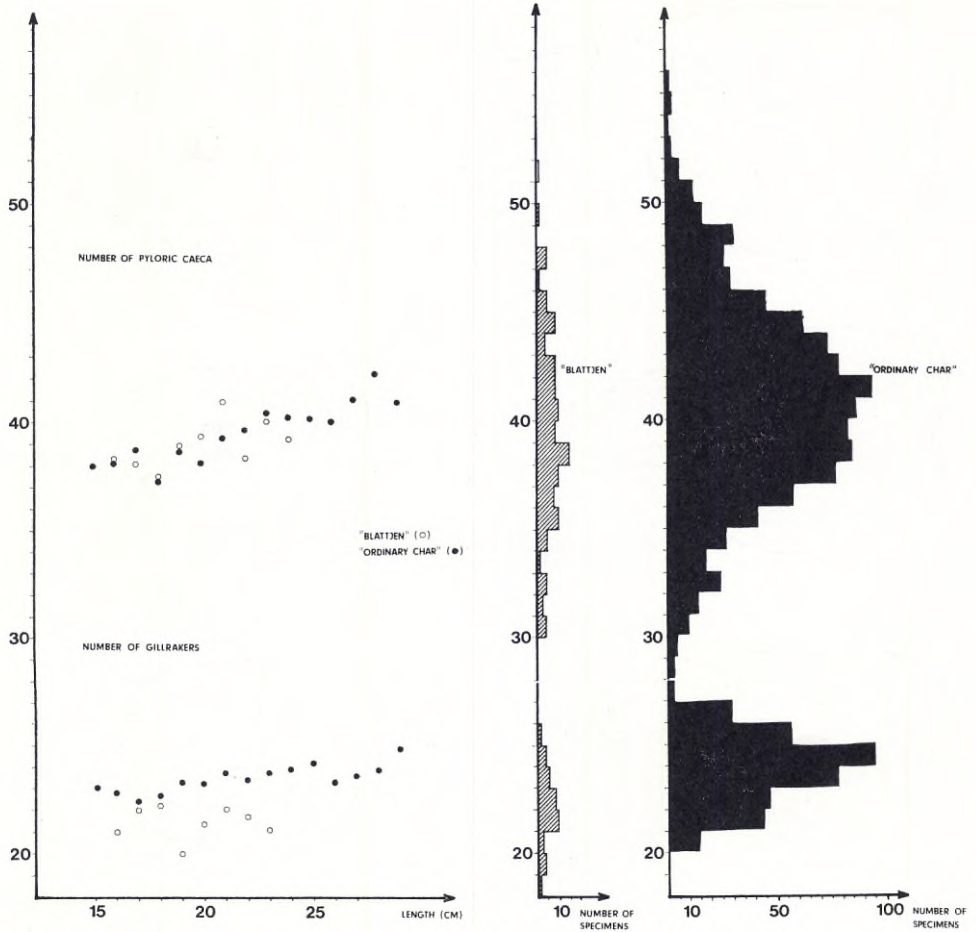
Fig. 2. Number of pyloric caeca and gillrakers of the two populations of char from Lake Övre Björkvattnet. Averages correlated to length of fish.

varies from 19 to 27, that of the "blattjen" from 19 to 23. The slight differ-ence seems real, but could not be used as a taxonomic character for identifi-cation.

McPHAIL (1961) found c. 25 gillrakers to be the mean for North American arctic char.

Pyloric caeca

The number of pyloric caeca of arctic char displays an extraordinary vari-ation. SAVVAITOVA (1969) reported the numbers to vary between 21 and 62 for the *Salvelinus alpinus* complex of Europe, Asia and North America. The number of pyloric caeca increases with length during the whole lifespan of the fish (RESHETNIKOV 1961).

Fig. 3. Flesh coloration of "blattjen" (left) and "ordinary char" (right). Size classes: 1 = < 150, 2 = 150—200, 3 = 201—300 mm. □ = white, ▨ = slightly pink, ▦ = pink.

Fig. 2 shows the char of Övre Björkvattnet to vary between 28 and 56, with a slight tendency for the average count to increase with the total length of the fish. No obvious difference between the "ordinary char" and the "blattjen" can be discerned.

Coloration at spawning time

The colours of the "ordinary char" are typical of the arctic char as a whole. During spawning time the back, the dorsal part of the head and sides

are dark grey-black. The belly, ventral fins and apical parts of the caudal fin are bright red, with very marked white margins on the ventral fins.

The "blattjen" does not seem to have any special spawning dress, but is dark violet with light-coloured belly and rather obvious parr marking all the year around. The ventral fins are pink, mostly not as deep red as with the spawning "ordinary char". As compared with immature "ordinary char" of the same size, the "blattjen" on the whole look plumper and darker.

The word "blattjen" has been interpreted as a dialectal form of the Swedish word *black,* which means: "of a weak and faded colour, bordering upon grey, black or reddish-yellow" (professor KARL-HAMPUS DAHLSTEDT, personal communication).

Flesh coloration

Red coloration in salmonids originates from dietary fat-soluble carotenoids (STEVEN 1948), and it seems that the consumption of crustaceans is the main cause of it.

Fig. 3 provides evidence for a relative difference in flesh coloration between the "blattjen" and the "ordinary char". Even when caught at the very same place with sinking nets in the littoral zone the "ordinary char" more frequently have "slightly pink" or "pink" flesh than do the "blattjen". The difference is difficult to explain as the main food of both forms has consisted of crustaceans — *Cladocera* for the "ordinary char", *Gammarus lacustris* for the "blattjen" (Fig. 5).

There is an evident tendency for bigger fish to have redder flesh than the smaller ones (*cf.* NILSSON and ANDERSSON 1967).

IV. Ecological characteristics

Habitat

In Table 1 are listed the numbers of "ordinary char" and "blattjen" caught at the bottom with sinking nets and pelagically with floated nets. A pronounced habitat segregation during the catch time (September—October) is evident, 75—94 per cent of the "ordinary char" having been caught with floated nets, 70—95 per cent of the "blattjen" with sinking nets.

Fig. 4 illustrates the habitat selection of the two populations of char as indicated by the depths of catch with sinking nets applied at the bottom and floated nets hung at two stations in the pelagic region of the lake. Apart from the fact that most of the "ordinary char" were caught pelagically, a tendency for a habitat segregation between the two forms in the littoral region can be discerned.

Table 1. The total numbers of "ordinary char" and "blattjen" caught with sinking nets and floated nets.

		Sinking nets		Floated nets	
		Char	Blattjen	Char	Blattjen
1964 n	....	43	42	328	2
%	....	11.6	95.5	88.4	4.5
1965 n	....	18	10	198	2
%	....	8.3	83.3	91.7	16.7
1966 n	....	14	47	232	8
%	....	5.7	85.5	94.3	14.5
1967 n	....	66	54	204	4
%	....	24.4	93.1	75.6	6.9
1968 n	....	27	12	406	5
%	....	6.2	70.6	93.8	29.4

Food habits and growth

Fig. 5 illustrates the food habits of the two types of char. To make possible a comparison from year to year, all samples were taken in autumn (late August—early October). At that time the fish of the subarctic lakes are well segregated into their feeding niches and subject to relatively little variation (NILSSON 1960). It should, however, be borne in mind that the food eaten in autumn need by no means be typical for the rest of the year.

In any case the present material reflects a pronounced food segregation between the two types of char in autumn, and approximately the same picture is obtained every year. The "ordinary char" has eaten *Cladocera* (especially *Daphnia galeata*) and terrestrial insects, but practically no bottom animals at all. The "blattjen", on the other hand, has specialized on bottom food, especially *Gammarus lacustris*. The *Cladocera* eaten by "blattjen" have mainly consisted of the half benthic *Eurycercus lamellatus*. A comparison between size classes does not yield much evidence for large variation. It is, however, noteworthy that in some cases the larger specimens of "blattjen" had eaten fish.

On the whole the food habits reflect the general habitat selection of the fish, planktonic crustaceans and terrestrial insects being more pelagic food than are *Gammarus, Lepidurus* and molluscs. A comparison between the "ordinary char" caught on the same sinking nets as the "blattjen" shows, however, that even there a similar food segregation can be discerned (Table 2).

Fig. 6 shows the growth rates of the two types of char (based on the analyses of otoliths of 1,877 "ordinary char" and 192 "blattjen") during the years 1964—69.

The highly significant difference in growth rate between the two forms shows rather little variation from year to year. The "blattjen" grows slowly
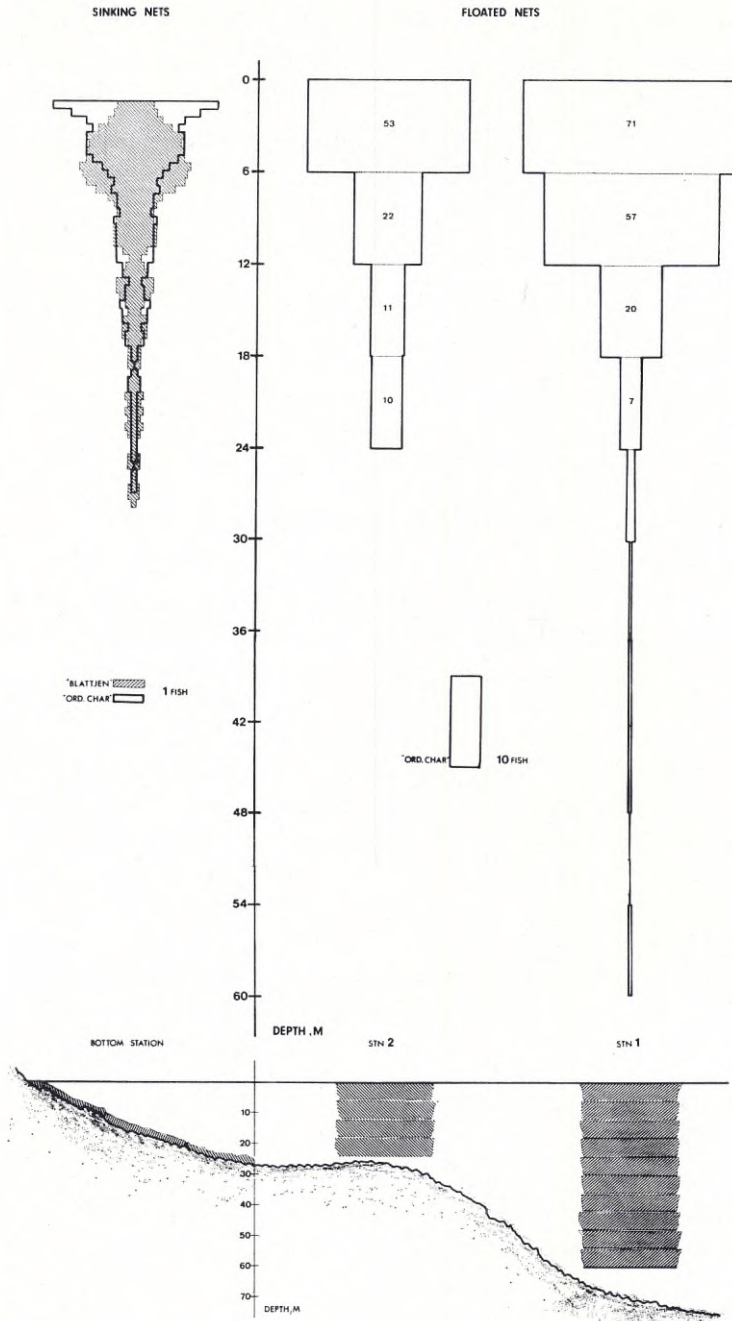
Fig. 4. Catch of "ordinary char" and "blattjen" at three stations, one close to the shore with sinking gillnets, one over shallow water with floated nets and one over deep water with floated nets.
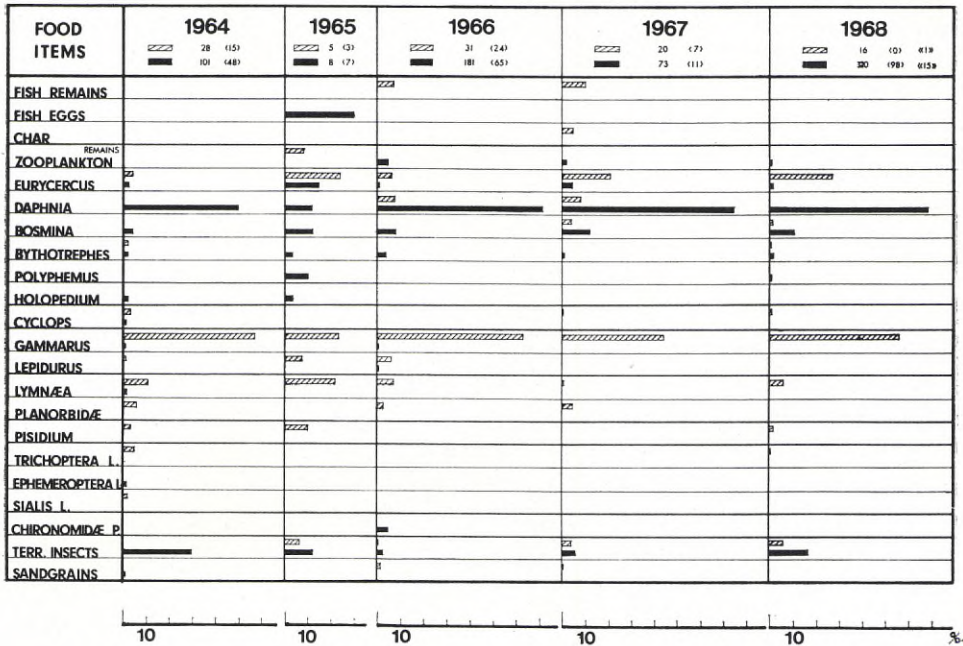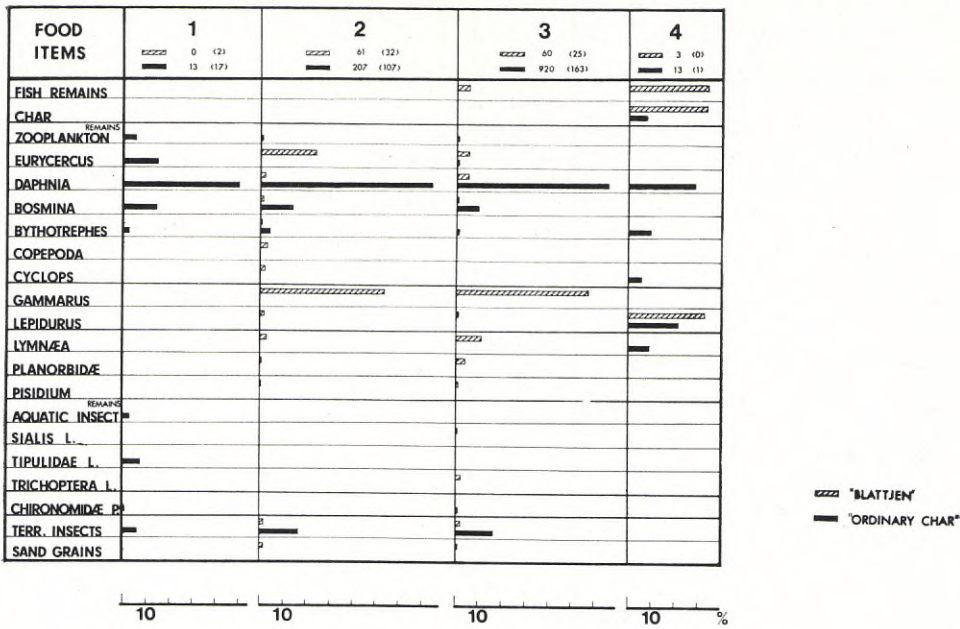
Fig. 5. Food habits of the chars of Övre Björkvattnet. Size classes (above): 1 = < 150, 2 = 150—200, 3 = 201—300, 4 = 301—400 mm.

Table 2. The food of "ordinary char" and "blattjen" caught with sinking nets in September 1964—68.

Food item	1964		1965		1966		1967		1968	
	Blattjen	Char	Blattjen	Char	Blattjen	Char	Blattjen	Char	Blattjen	Char
Fish remains	—	—	—	—	7.2	—	10.0	—	—	—
Fish eggs	—	—	—	9.9	—	—	—	—	—	—
Char	—	—	—	—	—	—	5.0	—	—	—
Plankton remains ..	—	—	8.0	—	—	—	—	—	—	—
Eurycercus	4.4	6.2	22.4	18.4	6.0	28.0	21.0	6.7	26.1	15.6
Daphnia	1.9	40.2	—	9.5	7.1	20.0	7.7	72.5	—	41.5
Bosmina	—	7.0	—	12.4	—	—	3.3	12.9	1.5	14.8
Bythotrephes	1.9	5.1	—	—	—	—	—	—	0.9	2.2
Polyphemus	—	—	—	11.5	—	—	—	—	—	—
Heterocope	—	—	—	—	—	—	—	—	—	0.2
Cyclops	3.7	6.4	—	—	—	—	0.4	—	0.9	—
Gammarus	55.9	3.4	23.3	—	66.7	20.0	43.8	2.2	60.4	2.2
Lepidurus	1.2	3.0	7.7	—	2.0	—	—	—	—	—
Lymnea	12.4	7.5	22.0	—	5.1	6.0	0.6	—	8.1	0.2
Planorbidae	5.7	0.1	—	—	3.2	6.0	4.2	—	—	—
Pisidium	3.7	—	10.0	—	—	—	—	—	1.5	—
Ephemeroptera larvae	—	7.2	—	—	—	—	—	—	—	—
Plecoptera larvae ..	—	—	—	—	0.1	—	—	0.2	—	—
Sialis larvae	2.9	0.3	—	—	—	—	—	—	—	—
Tipulidae larvae	—	3.6	—	—	—	—	—	0.1	—	—
Trichoptera larvae ..	5.6	—	—	—	—	—	—	—	0.6	—
Chironomidae pupae	—	0.3	—	—	—	—	—	—	—	—
Terrestrial insects ..	—	9.6	6.6	38.3	0.8	20.0	4.0	5.4	—	18.9
Sand grains	0.7	0.1	—	—	1.8	—	—	—	—	3.7
Plant remains	—	—	—	—	—	—	—	—	—	0.7
n	27	28	5	7	28	5	20	45	13	23

but attains on average a higher age. Of particular interest is the fact that all fish (both "ordinary char" and "blattjen") caught with sinking gill nets along the shores display a greater variation in growth rate than the fish caught pelagically with floated nets. This may reflect a general uniformity in planktonic as compared with benthic food. It might also indicate that there are fractions of the population of "ordinary char" that remain as littoral inhabitants for most of their time. The fact that in this case the form living on plankton has a higher growth rate may seem difficult to explain, especially as the main food of the slow-growing form is as substantial as that of *Gammarus lacustris*. To throw light on the question whether in spite of this the "blattjen" suffer from some sort of shortage of food, the degree of filling of the stomachs was noted.

The method used was simply that of classifying the stomachs as "empty", "nearly empty", "half filled" and "filled." Fig. 7 shows the result of this examination. It is obvious that during all years of investigation a larger share of the "ordinary char" had filled stomachs while the "blattjen" have mostly
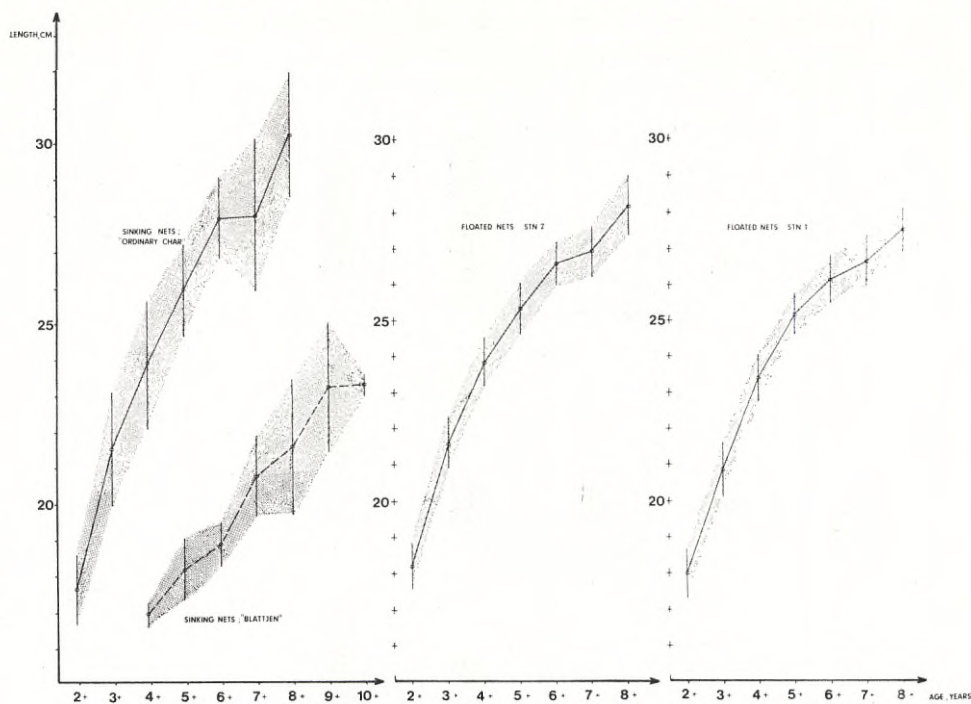
Fig. 6. The growth rate of "ordinary char" at three stations and "blattjen" at one station in Övre Björkvattnet. The stations represent an increased degree of pelagic habitat from left to right in the diagram. (cf. Fig. 4). Vertical lines represent standard deviation.

been classified as "half filled", "nearly empty" or "empty". It may thus be reasonable to suspect that the "ordinary char" have access to a richer supply of food than do the "blattjen", with a higher growth rate as result. In this context it should be noted that the "blattjen" to a large extent shares the biotope with the brown trout; in subarctic trout-char lakes the latter typically occupy the upper part of the littoral zone, where they feed mainly on bottom animals and terrestrial insects (NILSSON 1955, 1965). Table 3 shows that these habits are also valid for the trout of Övre Björkvattnet. It is interesting to note, however, that the food niche of brown trout is different from that of "blattjen", theoretically a result of interactive segregation (NILSSON 1965, 1967). In any case the "blattjen" seems to be pushed from two directions: the brown trout in the littoral and the "ordinary char" in the pelagic.

Future investigations may reveal which of the two populations of char will suffer the most severe competition from the recently invading whitefish. Table 4 shows the whitefish to be mainly planktivorous. The most important *Cladocera* eaten seems, however, not to be *Daphnia* as with the char, but more the semi-benthic *Eurycercus lamellatus*.
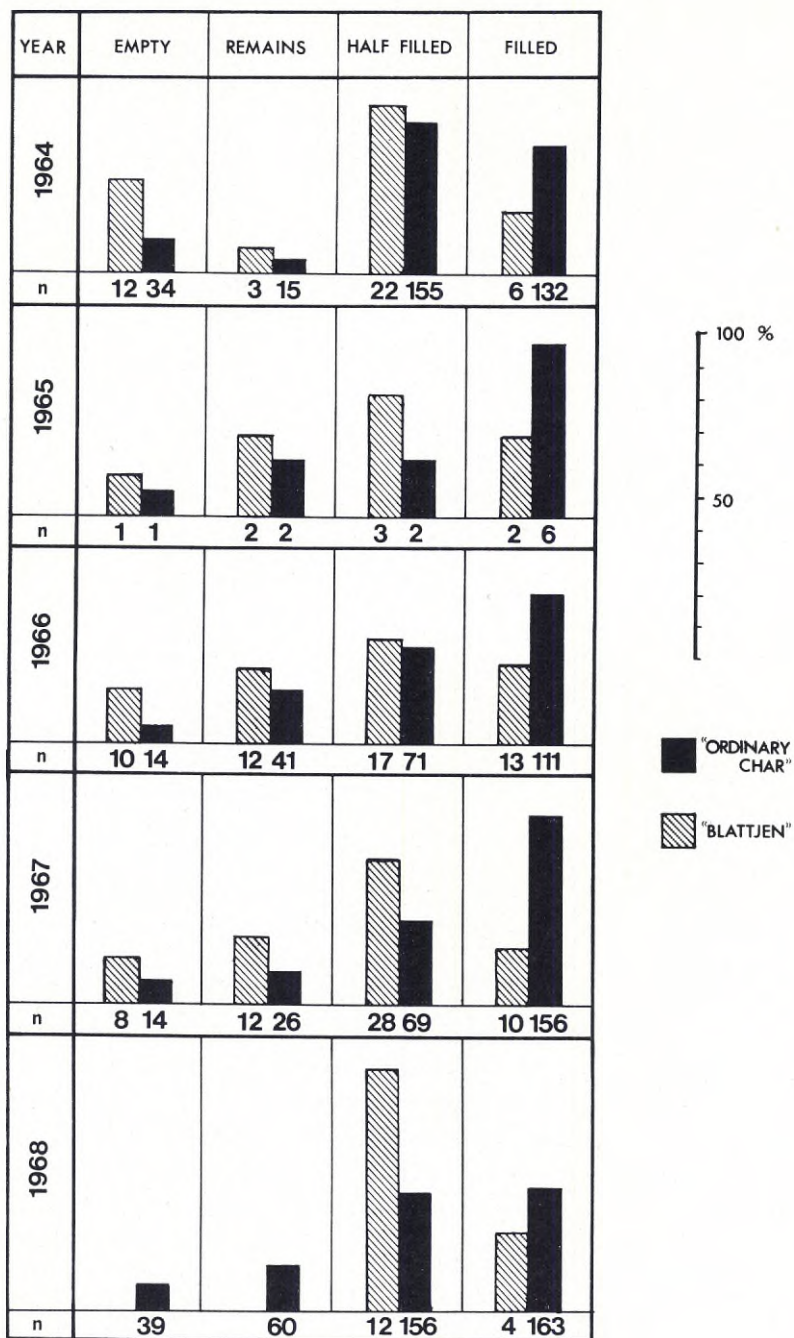
Fig. 7. Degree of filling of stomachs of the chars in Övre Björkvattnet.

Table 3. Food of brown trout caught in September 1964—68.

Food item	1964	1965	1967	1968
Fish remains	3.1	—	—	—
Eurycercus	—	8.5	1.3	—
Gammarus	9.6	2.4	8.9	2.1
Lepidurus	0.1	0.4	0.2	—
Lymnaea	1.4	—	—	0.6
Planorbidae	11.3	—	2.7	—
Valvata	—	—	0.4	—
Chironomidae larvae ..	1.8	—	2.7	—
Ephemeroptera larvae	1.6	—	2.5	—
Sialis larvae	0.9	0.7	—	—
Tipulidae larvae	4.4	—	1.9	—
Trichoptera larvae	18.8	2.0	48.8	9.5
Dytiscidae larvae	0.6	—	—	—
Plecoptera larvae	—	—	10.7	1.6
Chironomidae pupae ...	0.3	1.0	—	—
Trichoptera pupae	—	2.0	—	—
Ephemeroptera imago	6.0	—	—	—
Dytiscidae imago	—	—	0.7	—
Terrestrial insects	28.7	83.0	15.4	77.1
Oligochaeta	8.2	—	—	—
Sand grains	—	—	1.7	2.1
Plant remains	3.2	—	0.5	0.2
n	32	15	43	47

HANNERZ (1968) found that the "ordinary char" had lower radiocesium concentrations than the "blattjen", and interpreted this as a result of difference in food habits between the two forms.

Table 4. Food of whitefish caught in September 1964—68.

Food item	1964	1965	1967	1968
Plankton remains	4.8	8.8	30.1	9.3
Eurycercus	31.1	46.6	30.9	20.9
Daphnia	10.7	9.6	15.5	25.4
Bosmina	—	8.0	10.0	25.2
Bythotrephes	0.9	2.6	2.6	—
Holopedium	47.0	5.1	7.3	14.7
Gammarus	0.4	1.0	—	1.3
Lymnaea	2.3	5.1	1.0	—
Pisidium	1.9	0.3	0.1	0.1
Planorbidae	—	3.0	—	1.3
Mollusc remains	—	0.7	—	—
Chironomidae larvae ..	0.1	—	0.1	—
Coleoptera larvae	0.2	—	—	—
Dytiscidae larvae	0.1	0.3	—	—
Ephemeroptera larvae	—	0.2	—	—
Tipulidae larvae	—	5.4	—	—
Trichoptera larvae	—	—	1.7	—
Trichoptera pupae	—	2.6	—	—
Terrestrial insects	—	0.3	—	1.0
Sand and plant remains	0.5	0.4	0.7	0.8
n	20	33	39	80

Spawning and age at maturity

As a result of the difference in growth rate spawning "ordinary char" and "blattjen" have different average size when mature (Fig. 8). This should be an important isolating mechanism keeping the two populations apart during spawning time. The Figure also indicates that on average the "blattjen" matures at a later age than the "ordinary char".

It has hitherto been possible to spot the spawning sites of only the "ordinary char". Special test fishing in 1968 revealed the spewning of that form to occur in the period mid-September—early October. Even ripe specimen of "blattjen" were caught at the same time at the spawning sites of the "ordinary char". None of them, however, had running roe or milt, which indicates that the spawning of "blattjen" occurs at a later time.

V. Conclusions

The two forms of arctic char occuring in Lake Övre Björkvattnet obviously present very great differences in ecology (habitat and food selection), with resulting differences in growth rate and average size. Morphologically, also, the two forms show some slight differences, but it is very difficult to identify them by means of morphological characters alone. It is not established, but seems very probable, that the two populations are reproductively isolated. If so, the two populations present all the criteria of being different species as defined by MAYR (1963) and others, and thus SVÄRDSON's theory (1958) on the speciation of the Scandinavian chars is supported. It remains, however, to compare in all details other possible cases of sympatric sibling species of arctic char in the Palaearctic, as the present view is by no means distinct. Often, in those cases where there are two separate populations of char in the same lake, one is slow-growing and "black", the other more "ordinary". The slow-growing form, however, can be planktivorous as in Korsvattnet, or it can dwell in very deep water as in Blåsjön (NILSSON 1955). Nor can any general pattern as regards spawning habits be discerned. The presence or absence of interacting species, as well as many other factors, may play a part here. The possibility of introgression between the different populations resulting in different combinations of genes as in the genus *Coregonus* (SVÄRDSON 1970) is probably also of considerable importance. Further morphological analyses as well as serum protein analyses seems to be urgently needed. Such investigations should, however, always be accompanied by comparative ecological studies.
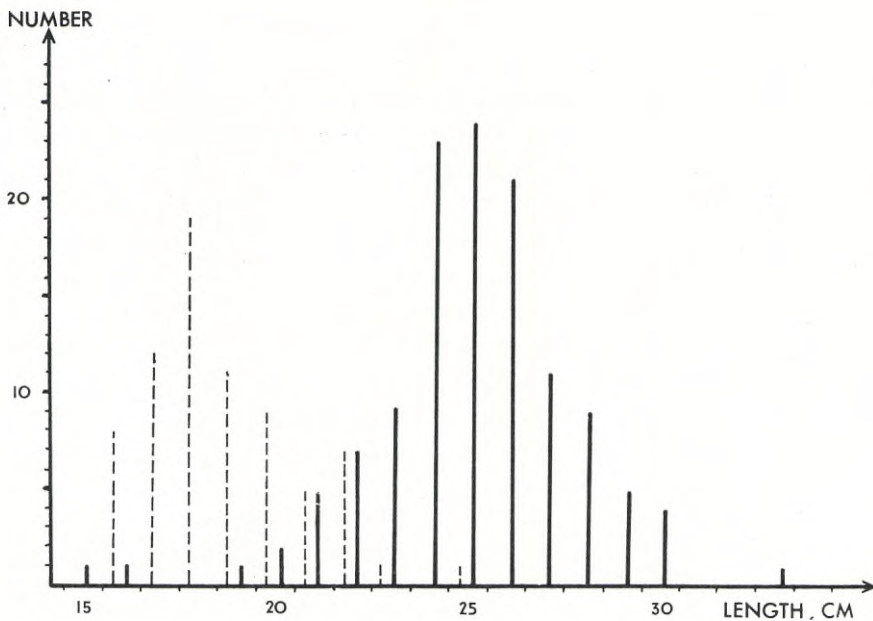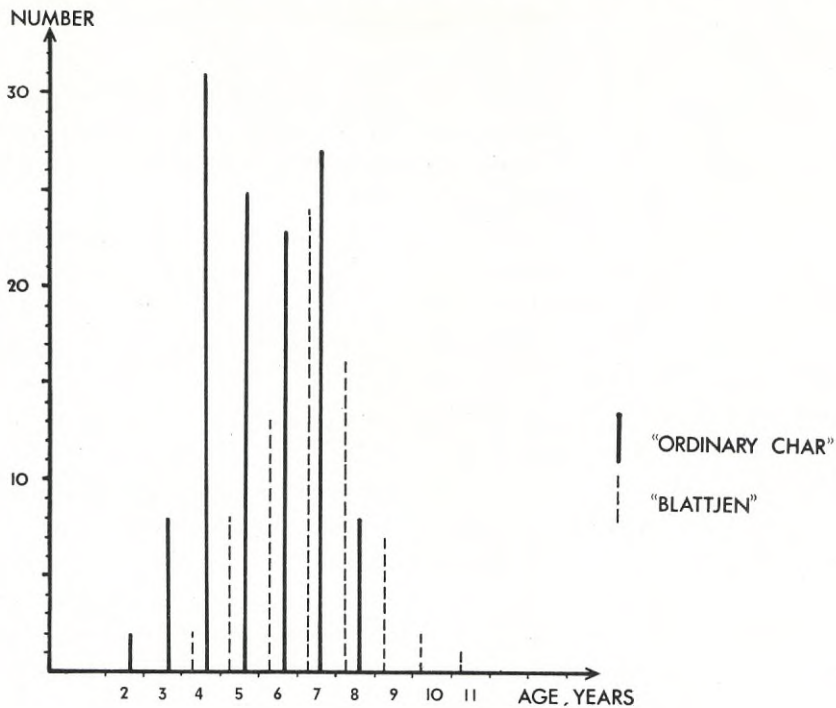
Fig. 8. Age and length at maturity of chars in Övre Björkvattnet.

VI. Summary

1. Several subpopulations of arctic char have long been recognized in Scandinavia both by local fishermen and by biologists. A description is given of two populations in a lake in southern Swedish Lappland, here referred to as "ordinary char" and "blattjen".

2. The two forms of char could be distinguished from the shape of their otoliths, one type being characterized as "arrow-shaped" (ordinary char), the other as "drop-shaped" (blattjen).

3. A slight difference in gillraker counts of the two populations could be discerned, but none for pyloric caeca.

4. Coloration of the two populations at spawning time is different, as is also flesh coloration in autumn.

5. Most "ordinary char" were caught with floated gill nets in the pelagic, most "blattjen" with sinking nets in the littoral region of the lake.

6. In autumn "ordinary char" fed on planktonic *Crustacea*, mainly *Daphnia*, while "blattjen" fed on bottom animals, mainly *Gammarus*. Even fish that were all caught at the same stations in the littoral region displayed a similar food segregation.

7. There is a highly significant difference in growth rate between the two forms, the "ordinary char" being more fast-growing than the "blattjen". "Ordinary char" caught with sinking gill nets as well as "blattjen" display a greater variability in growth rate than do char caught with floated nets.

8. A greater fraction of the stomachs of the "ordinary char" had a high degree of filling as compared with "blattjen". It is suggested that differences in stomach fullness as well as in growth rates results from a more severe competition between brown trout and "blattjen".

9. There was an evident difference in the average size of the spawning fish belonging to the different populations, the "blattjen" being smaller at maturity. On the other hand, they were on average older than the "ordinary char" at maturity.

10. The authors regard the two populations as being separate species. Although here are many parallels with the char populations of other lakes in Scandinavia, further analysis is needed before detailed generalizations as to the whole complex can be made.

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VIII. Addendum

While this paper was still in print, ANDERSSON, GUSTAFSON and LINDSTRÖM published an investigation on "double" populations of arctic char in two small lakes in the Central Swedish mountain region. In that case the fast growing species was predatory on the small one. A transplantation of both species into a third lake revealed that the difference in growth rate was manifest also in the new environment.

ANDERSSON, G., K.-J. GUSTAFSON and T. LINDSTRÖM. 1971. Rödingen i Rösjöarna på Fulu-fjäll. Information från Sötvattenslaboratoriet, Drottningholm (8). 18 pp.

Plasma esterases of some marine and anadromous teleosts and their application in biochemical systematics

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I. Introduction

The significance of molecular data to evolutionary history lies primarily in the tertiary semantides (Zuckerkandl and Pauling, 1965) which carry the genetic information.

Since most proteins and enzymes belong to this class they are well suited for taxonomic studies at various levels, and the polyphyletic branch of science which analyzes these characters — the biochemical systematics — has clearly illustrated the dynamic nature of the biological species, as defined by Mayr (1969).

If all possible protein recombinants are considered, intraspecific variation is so great that, as a matter of fact, each individual animal is biochemically and thus genetically unique (Medawar, 1957). Also at the sub-specific level, polymorphic loci may contribute to studies of population dynamics, because frequencies of certain proteins can be used to describe populations and may also show the extent of interbreeding and clines of gene flow (e.g. Sick, 1965; Koehn and Rasmussen, 1967). In some cases even sex-correlated differences may be encountered (Drilhon and Fine, 1963). The species specific properties of many proteins have revealed sibling species with a considerable amount of genetic distinctness where morphological divergency has been either very slight or considerable resulting in overlap of meristic characters (Dessauer et al., 1962; Manwell and Baker, 1963; Manwell et al., 1967; Nyman and Westin, 1968). Other proteins may suggest affinities at even higher taxonomic categories (e.g. Sibley, 1960; Dessauer and Fox, 1964; Nyman, 1966; Tsuyuki et al., 1968). For the study of evolutionary rates, however, it is important to realize that these rates may vary considerably from taxon to taxon even for homologous genes (Dessauer et al., 1962).

The inheritance mechanism of proteins may usually be demonstrated through hybrid analysis, both intra and interspecific, and because hybrids (F_1) usually display electropherograms which are summations of the parental

patterns, protein studies may add considerably to the knowledge of natural hybridization as well as the occurrence of speciation through hybridization (ABRAMOFF *et al.*, 1968; NYMAN and WESTIN, 1968; ASPINWALL and TSUYUKI, 1968).

The fact that certain proteins are affected by internal or external environment may also have diagnostic importance for studies of ontogeny, disease, diet or season (KOCH *et al.*, 1964; MULCAHY, 1967; VAN TETS and COWAN, 1966). From the above it becomes evident that '. . . a careful choice is to be made in order to consider only those proteins which are most appropriate for each special purpose.' (RABAEY, 1964). The objective of this paper is to illustrate the usefulness of blood plasma esterases to some of the taxonomic levels mentioned above in some marine and anadromous fish of the northern hemisphere.

II. Material

A total of 1245 fish belonging to 35 species was analyzed. Most of the marine species of fish were collected on the A. T. CAMERON cruises beginning in May 1969 through the summer 1970. Specimens of smelt and capelin were also obtained from other cruises and two samples of capelin (Middle Cove) were caught by handnet from the shore. Specimens of the Pacific salmon and rainbow trout were obtained at Nanaimo Biological Station, Vancouver Island and brown trout, brook trout and salmon specimens were obtained by angling in various Newfoundland waters. The systematic relationships of the species examined are given in Table 1. Classification and scientific names according to American Fisheries Society (1960), BERG (1941) and LEIM and SCOTT (1966).

Table 1. Systematic relationships of the species studies.

	Common name
Class *OSTEICHTYES*	
Order *CLUPEIFORMES*	
Family *SALMONIDAE*	
Genus *Salmo*	
Species *S. salar* LINNÉ	Atlantic salmon
S. trutta LINNÉ	brown trout
S. gairdneri RICHARDSON	rainbow trout
Genus *Salvelinus*	
Species *S. fontinalis* (MITCHILL)	brook trout
Genus *Oncorhynchus*	
Species *O. gorbuscha* (WALBAUM)	pink salmon
O. nerka (WALBAUM)	sockeye salmon
O. tshawytscha (WALBAUM)	chinook salmon
O. kisutch (WALBAUM)	coho salmon
O. keta (WALBAUM)	chum salmon
Family *OSMERIDAE*	
Genus *Mallotus*	
Species *M. villosus* (MÜLLER)	capelin
Order *NOTACANTHIFORMES*	
Family *NOTACANTHIDAE*	
Genus *Macdonaldia*	
Species *M. rostrata* (COLLETT)	spiny eel

Table 1 continued.

Order *GADIFORMES*
  Family *GADIDAE*
    Genus *Melanogrammus*
      Species *M. aeglefinus* (LINNÉ)   haddock
    Genus *Enchelyopus*
      Species *E. cimbrius* (LINNÉ)   fourbeard rockling
  Family *MACROURIDAE*
    Genus *Macrourus*
      Species *M. berglax* LACÉPÈDE   roughhead grenadier
    Genus *Coryphaenoides*
      Species *C. rupestris* GUNNERUS   rock grenadier
    Genus *Nezumia*
      Species *N. bairdii* (GOODE and BEAN)   marlin-spike
Order *PERCIFORMES*
  Family *SCORPAENIDAE*
    Genus *Sebastes*
      Species *S. marinus* (LINNÉ)   redfish
            S. mentella TRAVIN   redfish
  Family *COTTIDAE*
    Genus *Artediellus*
      Species *A. uncinatus* (REINHARDT)   hook ear sculpin
    Genus *Myoxocephalus*
      Species *M. scorpius* (LINNÉ)   shorthorn sculpin
    Genus *Triglops*
      Species *T. murrayi* GÜNTHER   mailed sculpin
    Genus *Cottunculus*
      Species *C. microps* COLLETT   polar sculpin
  Family *AGONIDAE*
    Genus *Aspidophoroides*
      Species *A. monopterygius* (BLOCH)   alligatorfish
  Family *CYCLOPTERIDAE*
    Genus *Cyclopterus*
      Species *C. lumpus* LINNÉ   lumpfish
    Genus *Eumicrotremus*
      Species *E. spinosus* (MÜLLER)   Atlantic spiny lump sucker
  Family *AMMODYTIDAE*
    Genus *Ammodytes*
      Species *A. dubius* REINHARDT*   sand launce
  Family *ANARHICHADIDAE*
    Genus *Anarhichas*
      Species *A. minor* OLAFSEN   spotted wolffish
            A. lupus LINNÉ   Atlantic wolffish
            A. denticulatus KRØYER   northern wolffish
  Family *ZOARCIDAE*
    Genus *Lycodes*
      Species *L. lavalaei* VLADYKOV and TREMBLAY**   arctic eelpout
            L. vahlii REINHARDT   Vahl's eelpout
Order *PLEURONECTIFORMES*
  Family *PLEURONECTIDAE*
    Genus *Reinhardtius*
      Species *R. hippoglossoides* (WALBAUM)   Greenland halibut
    Genus *Hippoglossus*
      Species *H. hippoglossus* (LINNÉ)   Atlantic halibut
    Genus *Glyptocephalus*
      Species *G. cynoglossus* (LINNÉ)   witch flounder
    Genus *Hippoglossoides*
      Species *H. platessoides* (FABRICIUS)   American plaice

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* *A. dubius* (offshore form) is sometimes considered con-specific with *A. hexapterus* PALLAS (inshore form) (*e.g.* RICHARDS, 1965).

** The four specimens analyzed were not examined microscopically, so confusion with *L. reticulatus* REINHARDT is possible. However, all specimens had identical zymograms, which at least indicates their con-specific origin.

III. Methods

Blood was withdrawn from the heart in heparinized capillary tubes, transferred to the polyethylene tubes of the Beckman Spinco Analytical System and centrifuged for 30 seconds after which the plasma was transferred to new tubes and frozen.

The electrophoretic cell is a horizontal type cooled by tap water. The discontinuous buffer system by ASHTON and BRADEN (1961) was employed and 11 % starch (Connaught Medical Res. Labs, Willowdale, Ont.) was used in the gels. A constant voltage of 400V was employed for 100 minutes, the current ranging from 225—100 mA. Incubation was performed in 0.2 M sodium phosphate buffer (BURSTONE, 1962) of pH 7.0. Non-specific esterase activity was obtained with a 1 % solution of α-naphthyl acetate (substrate) in equal amounts of distilled water and acetone and Fast Red TR salt as the diazonium coupler. Optimal enzyme activity was usually reached within a half hour.

For classification purposes the gels were exposed to the following substrates: naphthyl acetate (α, β), naphthyl propionate (α, β), naphthyl butyrate (α), naphthyl caprylate (α) and naphthyl laurate (α), all of them 1 % solutions in distilled water and acetone.

Inhibition studies were performed by exposing the gel strips to various molar solutions of inhibitor substances, dissolved in a buffered saline, for 20 minutes, whereafter the staining solution (also containing inhibitor in the same concentration as that during the inhibitor reaction — according to KNOWLES et al., 1968) was added. The following inhibitors were used: DFP (diisopropylfluorophosphate), eserine sulphate, p-HMB (p-hydroxymercuribenzoate) and dichlorvos (2.2-dichlorovinyldimethylphosphate). Classification of esterase sub-classes was performed according to the inhibition pattern by AUGUSTINSSON (1961). Gels were photographed and measured after a two hours fixation in a 5:5:1 solution of methanol, distilled water and acetic acid.

IV. Results and discussion

Esterases are by definition enzymes which catalyze the following reaction: $R\text{-}COOR' + HOH = R\text{-}COOH + R'OH$. The large class of hydrolytic enzymes which has these properties is widely distributed in nature (BURSTONE, 1962). Their physiological function is manifold and they are involved in regulatory processes and may also play a role in protein metabolism (MYERS et al., 1957). Blood serum esterases in teleosts are well suited for systematic studies by electrophoretic methods, because, despite their heat lability, they can withstand months and sometimes years of storage (in a frozen state) and

may even become dehydrated without blurring their tertiary structure. Another advantage for electrophoretic studies is their tolerance against interaction with other protein molecules, such as haemolysation products, which means that they can be readily visualized in blood from frozen fish (see for instance Fig. 2 B). Also, electrophoretic separation is facilitated by the fast anodic migration of most fish esterases, which keeps them out of the slow-moving haemoglobin spectrum.

The results of the esterase analysis are separated into six classes, *viz.* (1) esterase classification, (2) intraspecific variation, (3) species specificity, (4) generic similarity, (5) family similarity and (6) hybridization.

Esterase classification

Inhibition studies

All esterases were insensitive to both high (p/*=3.00) and low (p/=5.00) concentrations of eserine sulphate and p-HMB, but were more or less completely inhibited by high concentrations (p/=3.00) of dichlorvos and DFP. These properties are characteristic of carboxylesterases (ali-esterases), which are resistant to eserine but are inhibited by organophosphates (AUGUSTINS-SON, 1961). Inhibition by both eserine and organophosphate (indicative of choline esterase) or by p-HMB alone (arylesterase) was not observed in any case. However, there is an extensive variation in tolerance to organophosphates. One extreme is present in arctic eelpout, (*Lycodes lavalaei*), which was only slightly inhibited by both DFP and dichlorvos in high concentrations (p/=3.00), the other extreme taken by the Salmonidae, the esterases of which were completely inhibited by low concentrations (p/=5.00) of the same compounds.

Substrate specificity

Comparisons of enzyme reaction rates indicated a selective affinity for short-chain naphthyl esters and more specifically for the alpha-isomers of naphthyl acetate and naphthyl propionate. In most families the reaction rates for hydrolyzing propionyl and acetyl esters were almost identical, among the Salmonidae a slightly faster reaction was obtained with the propionyl ester.

These studies indicate the predominance of carboxylesterases (EC 3.1.1.1, carboxylic ester hydrolase) in the sera of fish, with a selective affinity for alpha-isomers of naphthyl acetate and naphthyl propionate, which agrees with earlier studies (AUGUSTINSSON (1961); KOEHN and RASMUSSEN (1967); RIDGWAY *et al.* (1970) and NYMAN (1970). Also, there is generally a close association between the serum esterase mobility and the serum albumin fraction.

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* (negative logarithm of the molar concentration of inhibitor solutions).
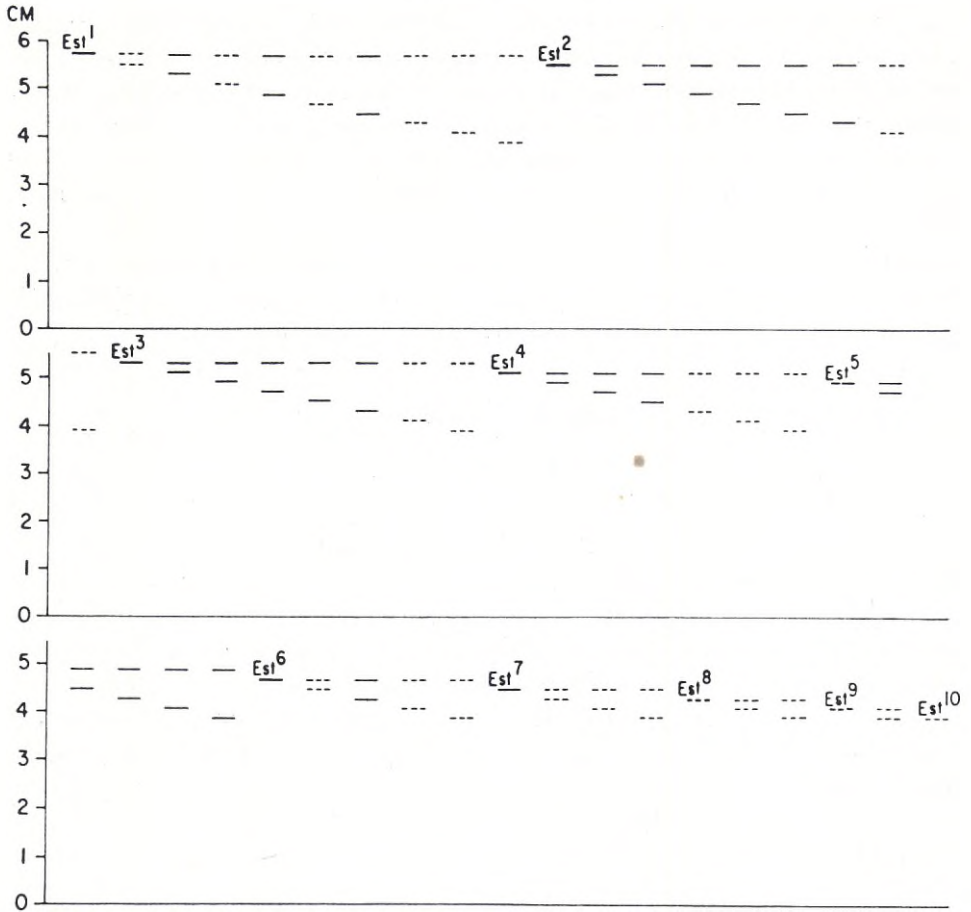
Fig. 1. Plasma esterase phenotypes in capelin. Zymograms indicated by broken lines have not yet been found because of low allele frequencies. Est^1-Est^{10} represent the various homozygous patterns. The scale to the left indicates the anodic migration in this and all following figures.

Intraspecific variation

One locus, several alleles

This is the common type of intraspecific variation in blood serum esterases of fish and occurs in roughly 1 species out of 5 (NYMAN, unpublished data). It consists of a polymorphism determined by the combination of a number of different alleles at a locus. This mode of inheritance is well substantiated through numerous population studies and breeding data in a great variety of organisms. The resulting phenotypes appear as either one- or two- or more band zymograms, representing homozygous and heterozygous allele com-
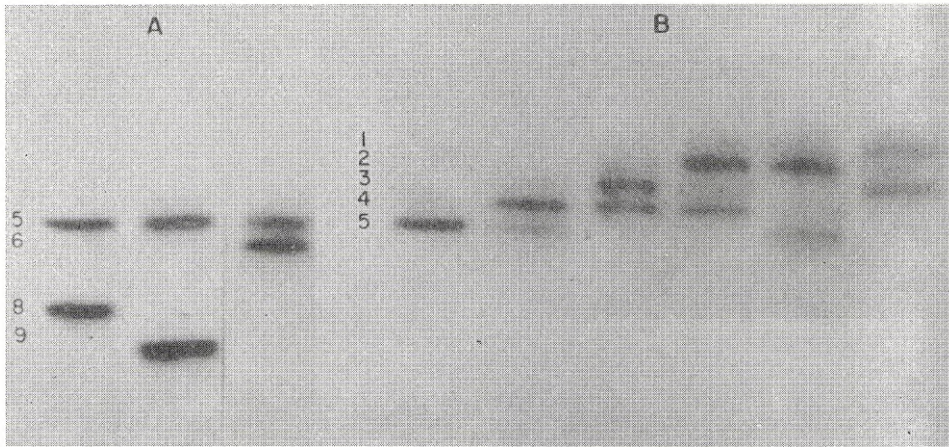
Fig. 2. (A) Three zymograms obtained from fresh capelin plasma. (B) Six zymograms from frozen whole blood after roughly six monhts storage. Numbers to the left of each photograph indicate relative position of the various alleles.

binations, respectively. This type was found in capelin (*Mallotus villosus*), where at least ten alleles are involved in the polymorphism (Fig. 1). The minimum number of possible phenotypes will thus be 55. Only 30 of the theoretically possible combinations were encountered because of the small sample size and the rarity of some of the alleles, for instance the probability of finding homozygous Est[9] and Est[10] phenotypes is less than 1 in 100,000.

Three heterozygous phenotypes are shown in Fig. 2 A. These zymograms are obtained from freshly sampled blood plasma. In Fig. 2 B six phenotype classes are indicated as revealed after staining of whole blood from deep frozen fish. Freezing and mixing with haemolysation products obviously does not interfere with the enzyme kinetics.

More than one locus

In sand launce (*Ammodytes dubius*) the esterase zymogram comprises at least two polymorphic loci with no linkage. The resulting zymograms are thus highly variable and illustrate the importance of analyzing large numbers of specimens in species with complex polymorphisms. If this variability had not been known an investigator faced with the three specimens typed in Fig. 3 possibly would have classified them as morphological sibling species. This situation, however rare, calls for multiprotein analysis in all doubtful cases. No gene frequency data could be obtained due to the low number of fish (15) available.
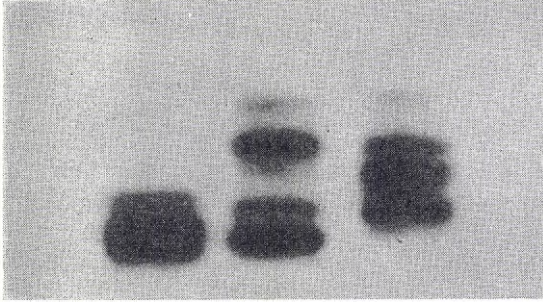
Fig. 3. Different zymograms in sand launce.

'Diffuse' variation

The esterase zymograms in redfish (*Sebastes mentella*) consist of a single broad zone which is both blurred and low in enzyme activity. Although the width of this zone remains more or less the same, its position displays a considerable amount of variation (Fig. 4). This variability could be attributed to the action of polygenes, however, this variability overlaps completely the zymograms of another redfish species (*Sebastes marinus*).

Species specificity

Apart from a few instances among the Salmonidae and the two sibling species of redfish (*Sebastes*) all serum esterases appeared species specific. This is illustrated by Fig. 5 which shows zymograms of six species with different types of zymograms, monomorphic esterases with bands of different width and position and more complex patterns with minor bands adjoining the main zone of activity.
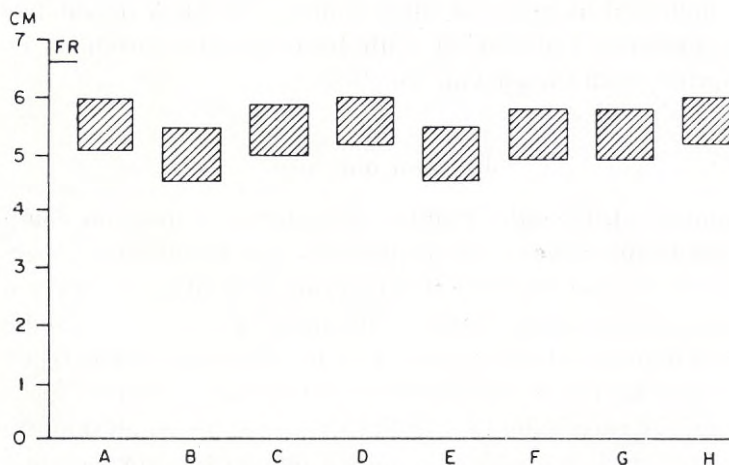
Fig. 4. Variability of redfish zymograms.
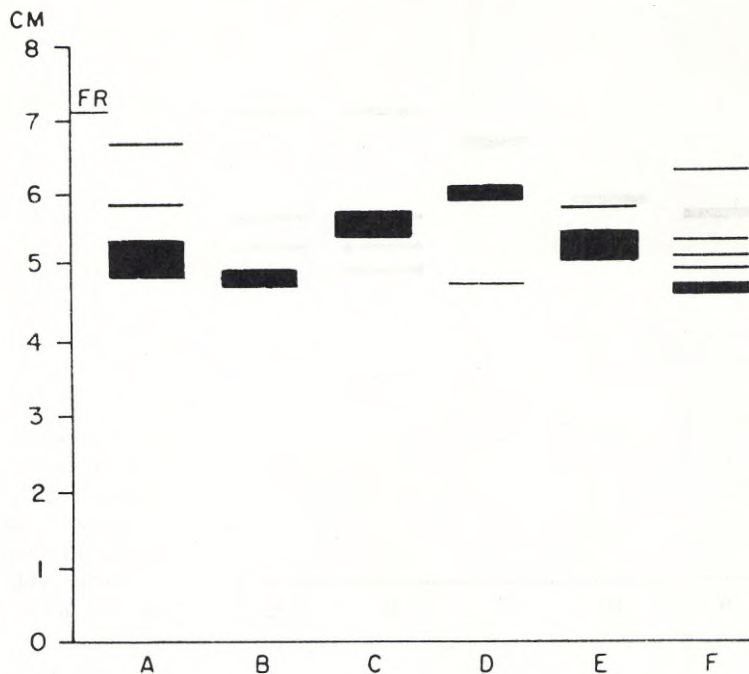
Fig. 5. Species specific zymograms in (A) spiny eel, (B) lumpsucker, (C) spiny lumpfish, (D) haddock, (E) 4-bearded rockling and (F) alligatorfish.

Generic similarity

Similarity of species belonging to the same genus

The three species of the genus *Anarhichas* (wolffishes) here analyzed each have only one molecular form of serum esterase, which appears as a single band with different genetic coding and thus different position in the zymograms (Fig. 6). The close similarity in position of species 'A' and 'B' does not indicate that these are more closely related to one another than either of them to species 'C', because with other molecular properties identical, it is the net charge of the protein that determines electrophoretic mobility. This means that substitution of a single amino acid may have a considerable effect on the mobility of a band, whereas losses or gains resulting from several mutations may not affect the net charge at all and thus not the mobility either. However, the stage of things found in the genus *Lycodes* (eelpouts) (Fig. 6 D and E) gives more information on hereditary divergence, because we may here have a basic conservative pattern, which could be genus or even family specific, and species specificity is maintained through losses or additions of certain alleles. Unfortunately only two species of this genus were analyzed so nothing can be stated as to the extent of this variability.
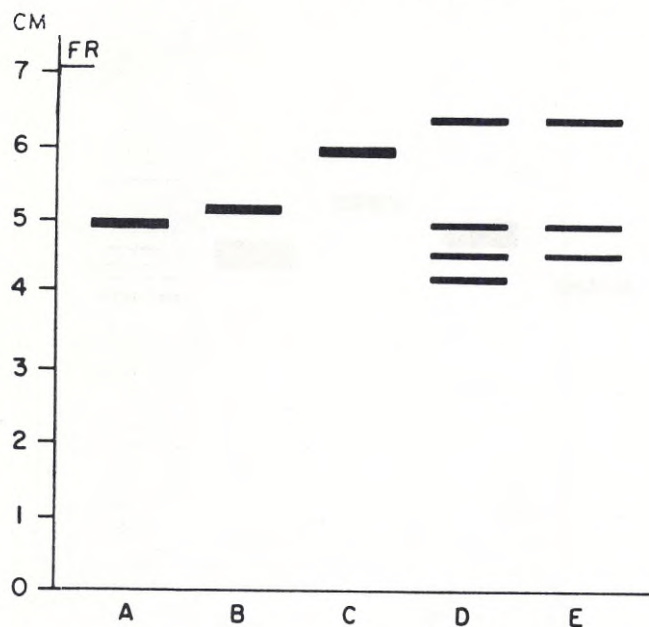
Fig. 6. Generic similarity in wolffishes (A—C) and eelpouts (D, E). A=spotted wolffish, B=Atlantic wolf-fish, C=northern wolffish, D=arctic eelpout, E= Vahl's eelpout.

Relationship of genera within the same family

Above (Fig. 6 D and E) it was shown that there may exist a basic pattern which indicates a relationship between genera. In some families this may be complicated by the presence of several 'basic' patterns which reflect groupings of interrelated genera at the sub-family level. In the family Pleuronectidae, for instance, there is a major esterase zone common to both Greenland and Atlantic halibut (*Reinhardtius hippoglossoides* and *Hippoglossus hippo-glossus*) (Fig. 7 A and B). Species differences are found in minor bands. However, witch (*Glyptocephalus cynoglossus*) and plaice (*Hippoglossoides platessoides*) of the same family have another basic pattern in common, which consists of two bands, none of which corresponds in mobility to the single group-specific zone in Greenland and Atlantic halibut (Fig. 7 C and D). Species specific properties are maintained in the same manner as in halibut and turbot, *i.e.* variability in number and position of minor bands. Besides, one of these zones in plaice displays extensive variation (Fig. 7, 'a').

Family similarity

The first report of intra-family similarity in esterase zymograms of fish concerned a comparison between the families Salmonidae and Cyprinidae (NYMAN, 1966). In the present study representatives of three families, viz. Salmonidae, Cottidae and Macrouridae, are compared (Fig. 8). The conserva-
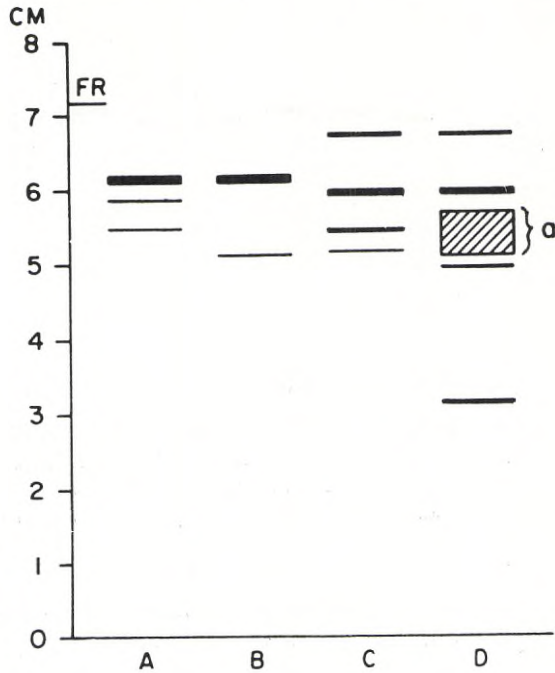
Fig. 7. Groupings of genera within the same family (*Pleuronectidae*). A=Greenland halibut, B=Atlantic halibut, C=witch flounder, D= American plaice.

tive zymogram among the Salmonidae consists of one band, rather broad and with high enzymatic activity. Only one of the 12 species so far studied in this family had a polymorphic esterase (the char: *Salvelinus alpinus* L.), but insufficient numbers of specimens of the *Oncorhynchus* species tested in this study may have prevented detection of polymorphisms. The Salmonidae is one of the very few families where esterase zymograms are not necessarily species specific (see also the genus *Catostomus*, KOEHN and RASMUSSEN, 1967). Whether this similarity depends on restricted tolerance of the homeostatic factors or rather loci with very low mutability is unknown, also, the identical electrophoretic mobilities frequently encountered may not necessarily be the result of enzyme homology, even if this appears to be the case among the *Salvelinus* (NYMAN, 1967). For classification purposes, for instance for the detection of hybrids, other enzyme systems as well as the total blood serum electropherograms (Amido Black) are distinctly species specific in all species so far studied. Among the Cottidae the range of variations is wider (Fig. 8 H—K) but one case of species overlapping has been discovered (NYMAN and WESTIN, 1969). The enzyme activity is lower in this family than in the Salmonidae, but although the bands are very thin they are also sharply defined. Also, among the Cottidae the zymograms may exhibit more than one molecular form of esterase. Although the three species of grenadiers (*Macrouridae*) analyzed are placed in different genera they have
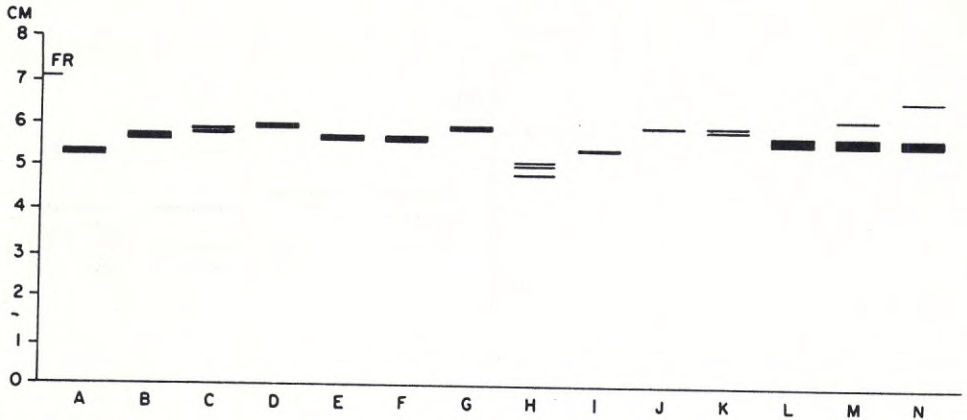
Fig. 8. Family similarity in *Salmonidae* (A—G), *Cottidae* (H—K) and *Macrouridae* (L—N). A=brown trout, B=Atlantic salmon, C=brook trout, D=rainbow trout, E=pink salmon, F=chinook salmon, G=coho salmon, H=polar sculpin, I=shorthorn sculpin, J=mailed sculpin, K=hook ear sculpin, L=roughhead grenadier, M=rock grenadier, N=marlin-spike.

a conservative pattern in common which comprises a broad band of high enzyme activity (Fig. 8 L—M). Species and probably genus specificity is here maintained in a manner similar to those described above among eelpouts and the two groups of pleuronectids, with a homologous and homozygous locus which in the case of grenadiers appears to be a family-indicator, and one or more variable loci, possibly with different fixed homozygotes, since no intraspecific variation was noted. The genetic stability of for instance the Macrouridae and *Lycodes* examined in this study contrast strongly the fast evolutionary changes among Salmonidae and Cottidae, and thus support the views of SIMPSON (1964) and RICHMOND (1970) that molecular evolution does not proceed at a constant speed for any particular protein.

Hybridization

No natural hybrids were encountered in this survey. The most typical mechanism of enzyme inheritance, co-dominance (NYMAN, 1970), is however reflected in an artificially produced hybrid between chum and chinook salmon (Fig. 9). With co-dominance one allele from each of the species specific and usually homozygous genes of both parental species is inherited in the F_1-hybrid, which thus in general exhibits a complete summation of the zymograms of the parents with roughly half the concentration for the species specific bands (NYMAN, 1970). Since a polymorphic locus might give the same result we would have to examine additional protein systems in such cases. This simple mode of inheritance is of course of great importance for the detection of natural hybrids, especially among morphological sibling species with overlapping meristic characters.
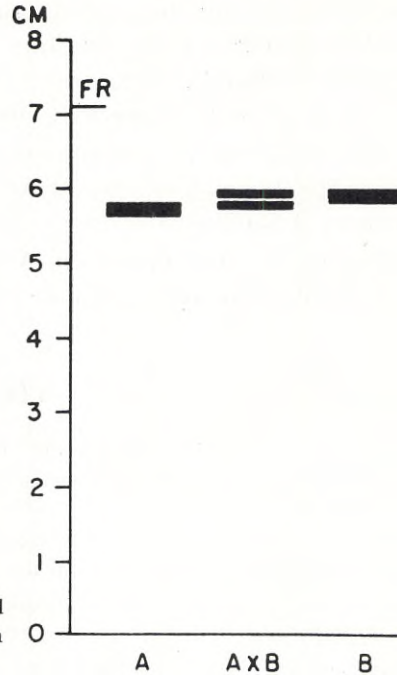
Fig. 9. Co-dominant relationship of genes as revealed by a study of an artificial F_1 hybrid. A=chum salmon, B=sockeye salmon, A$\times$B=hybrid.

V. Summary

This paper presents a survey of the serum esterases of 35 species of marine and anadromous fish. With few exceptions these enzymes appear to be species specific and agree with classical taxonomy. Also, certain trends in the phylogeny of the taxa involved are indicated, which clearly illustrate the differential rates of evolution among taxa at the same category level and the different modes of genetic changes that may occur. According to inhibition studies and substrate specificity the serum esterases of these marine teleosts can be classified more specifically as carboxylesterases (formerly aliesterases; EC 3.1.1.1 carboxylic ester hydrolase) with a selective affinity toward alpha-isomers of naphthyl acetate and naphthyl propionate.

VI. Acknowledgments

Cameron, and for these latter samplings thanks are due especially to Messrs G. H. WINTERS, A. T. PINHORN and A. M. FLEMING, all of the Biological Station, St. John's, Nfld. One of the samples of spawning capelin was caught by Mr A. MURPHY whose assistance was most appreciated.

For help with the classification of most of the uncommon species I owe many thanks to Messrs R. WELLS, E. M. LEGROW and E. J. SANDEMAN of the Biological Station, St. John's.

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The *Cestoda* fauna of the genus *Coregonus* in Sweden

By Åke Petersson

Contents

I. Introduction

In Sweden the occurrence of *Cestoda* in freshwater fish is of current interest because of the suggestion that the numerous lake regulations would increase the distribution and abundance of tapeworms. The question whether the regulation of a lake can influence the frequency of *Triaenophorus crassus* FOREL prompted the present investigation, since the presence of *T. crassus* in the flesh of whitefish reduces the latter's economic value.

In particular, the relation of the parasite fauna to different species of whitefish will be elucidated.

There are few investigations concerning the cestode fauna of freshwater fish in Scandinavia and Finland: in Sweden NYSTRÖM (1863), OLSSON (1893), LÖNNBERG (1892), BERGMAN (1923), NYBELIN (1922, 1925, 1931), LAWLER (1969) and PETERSSON (1971), in Norway HUITFELDT-KAAS (1912, 1916, 1927), SÖMME (1941) and VIK (1954, 1957, 1958, 1959, 1963), in Finland JÄRVI (1909) and WIKGREN (1956, 1963, 1964). There is one major paper dealing with the parasite fauna of the genus *Coregonus* (ZSCHOKKE 1933).

According to SVÄRDSON (1949, 1950, 1952, 1953, and 1957) there are in the Palaearctic seven species of *Coregonus*. Secondary introgression has had the result that the morphological characters have to a large extent dissappeared while the ecological ones remain. However, the number of gillrakers constitutes a phenotypical, non-variable morphological character that makes it possible statistically to distinguish the species from each other.

The ecological differences between the species are of great interest when one is examining the composition and variation of the parasite fauna.

The nomenclature in SVÄRDSON (1957) is used.

II. Areas investigated and material obtained

Whitefish samples from 61 localities were examined. The localities range from Lake Torneträsk 68°20′N in the north to Lake Ringsjön 55°50′N in the south (Figs. 1 and 2). The material was collected during the years 1959—68. It is put together in tabular form in Table 1.

Examinations were made in three different forms:

1. Dissection of the whole fish.
2. „   of the muscles.
3. „   of the internal organs and abdominal membranes.

Protozoa, except for *Henneguya* (GURLEY), and monogenea trematodes have not been taken into account.

In all 6,921 whitefish were examined. In 1,620 cases the whole fish was examined and in 3,470 specimens the presence of all *Cestoda* was noted. Infestations of parasites in the flesh were examined in 6,176 fishes.

III. Methods

The sampling of whitefish was carried out mainly with gill nets of different mesh sizes in order to obtain fish of various sizes. On some occasions seine nets were used.

In most cases the fish were examined after they had been frozen.

Parasites in the flesh were found by cutting the fish into fillets thin enough for the flesh to be translucent. The autopsy of the intestines and the internal organs was carried out under a binocular lens.

The parasites were fixed in formol, inert heated formol or formolalcohol. Total and section preparations were stained in haematoxylin-eosin or eosin.

IV. Species of *Cestoda* analysed

The finds have been entered in summary in the text, and have also been summed up in the maps (Figs. 4—7).

Most of the parasites were found in nearly all species of whitefish. When a parasite was found in only one species, for example *Eubothrium salvelini* (SCHRANK), this may be because the parasite is very rare. However, it is probable that any species of whitefish can be infested.
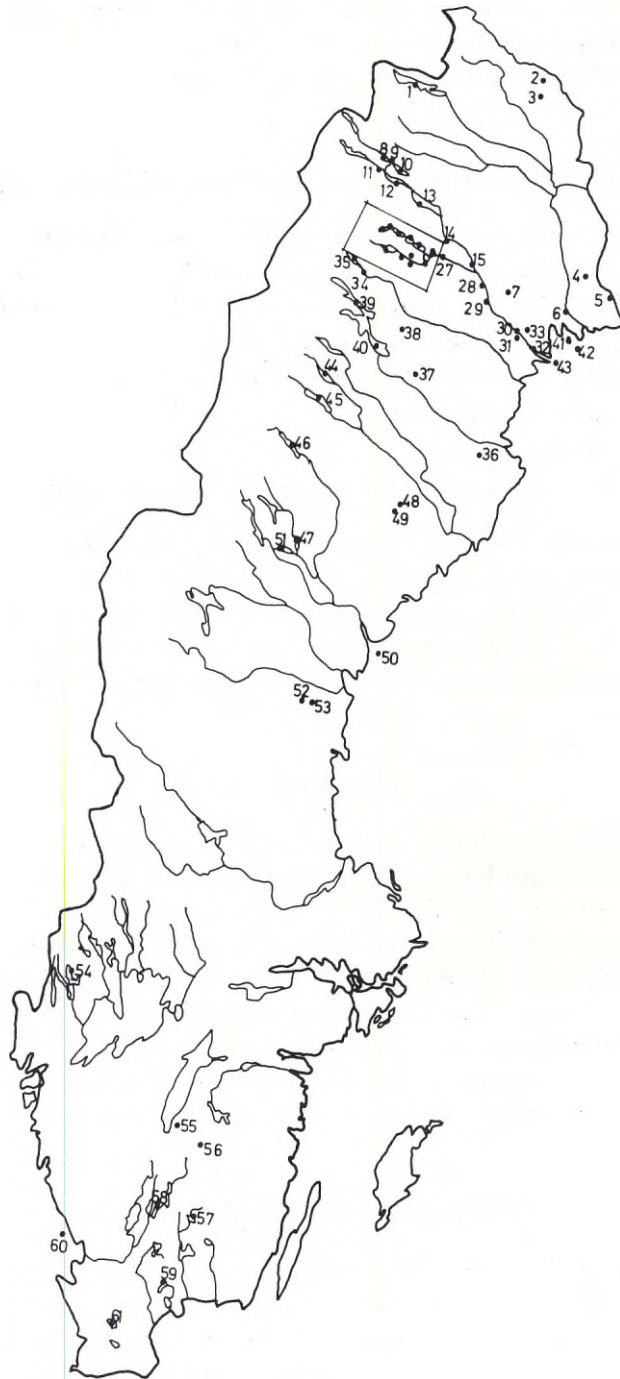
Fig. 1. Distribution of the field stations where collecting was carried out. The boxed area encloses the Lilla Lule älv river, cf. Fig. 2. Figures, see Tab. 1.
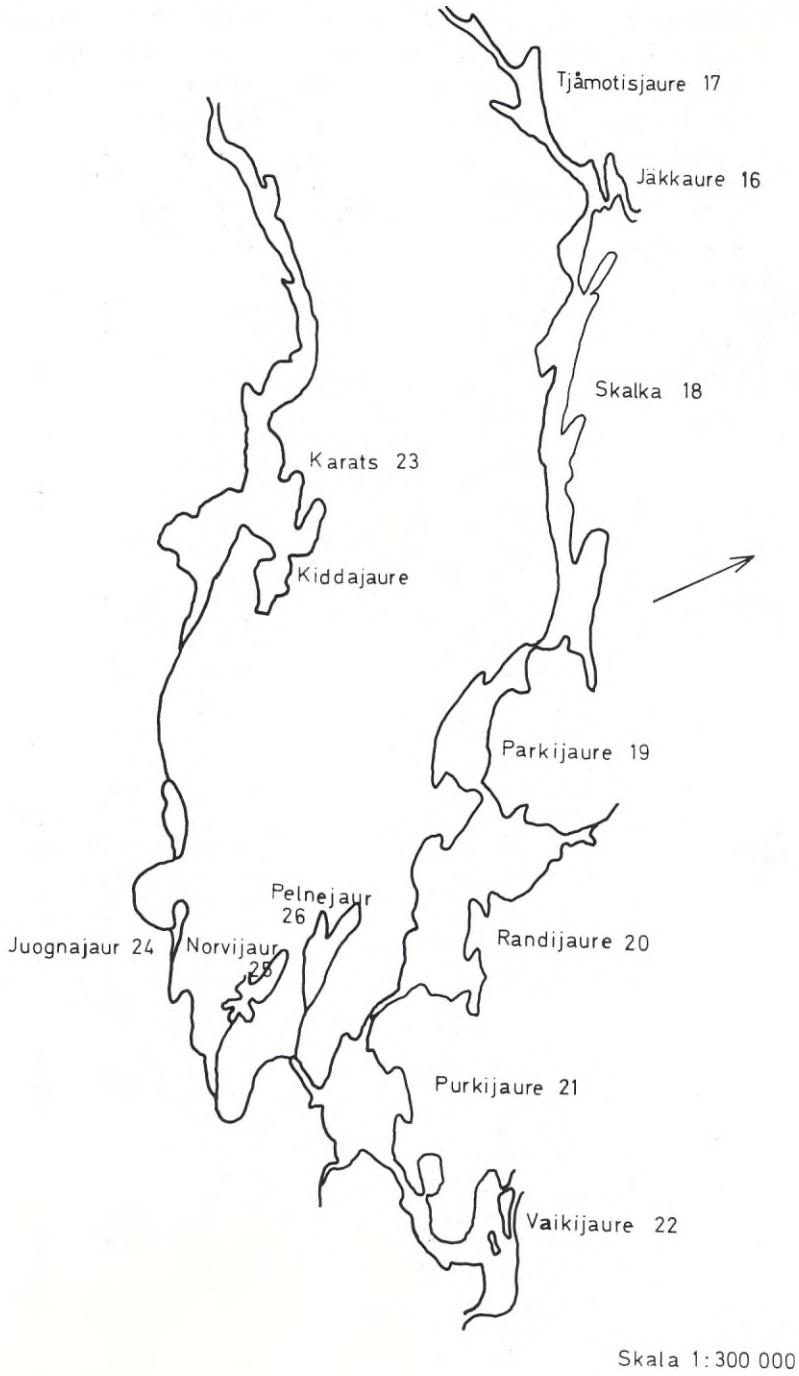
Fig. 2. Map of River Lilla Lule älv. Figures, see Tab. 1.

Table 1. Localities (Cf. Figs. 1 and 2), species of whitefish, total number of whitefish examined, and type of investigation. The habitats are indicated by L (lake), S (coastal area) and R (river). Type of dissection: T (total dissection), M (muscles examined), V (viscera examined).

No. cf. Fig. 1	Locality	Habitat and month	Species of whitefish	Number of gill-rakers	No. of whitefish examined	Kind of investigation
1	Torne träsk	L IX -61			13	M
2	Paitasjärvi	L IX -65	C. lavaretus	26—30	10	M
3	Sudajärvi	L X -65		19—25	60	M
4	Puostijärvi	L X -65			10	M
5	Kukkola	R VIII -62	C. lavaretus	26—35	50	M
6	Kamlunge	R VIII -62	C. lavaretus	26—34	52	M
7	Sandträsk	L IX -62	C. albula		81	M (T 15)
8	Kakerjaure	L IX -62		25—34	82	M
9	Pätsats	L IX -61		23—40	50	M
	"	IX -66		25—40	47	M
10	Satisjaure	L IX -60		26—40	108	M
	"	IX -61		26—40	138	M
	"	IX -66		26—43	33	M (T 23)
	"	VIII—IX -67		21—47	264	M (T 55)
11	Kårtjejaure	L VIII -62		27—38	20	T
12	Langas	L X, XII -62		23—37	76	M (T 26)
		I—XI -63		25—41	105	T
13	Lulejaure	XII -60		23—40	30	M
	"	X -62		20—43	190	M (V 143)
	"	X, XII -63		21—43	248	M (T 36)
	"	X -65		24—44	120	M, V
14	Ligga	R VI -62	C. lavaretus	30	34	M
15	Porsi, Kalludden	R V -62		25—34	36	M
	" —	VI -67		22—34	102	M
16	Jäkkaure	L XI -65	C. pidschian	19—22	69	M (T 19)
17	Tjåmotisjaure	L VI, VIII -64	C. pidschian	18—24	67	T
18	Skalka	L VII, X -61		18—54	108	M, V
	"	VIII -64	C. pidschian	19—23	47	T
	"	VI -66		19—27	35	T
	"	IX -67		18—27	40	T
19	Parkijaure	L IX -61	C. peled		29	M, V
	"	VIII—IX -66		18—54	92	M (T 30)
		-59		18—53	167	V
20	Randijaure	L VIII—IX -61		18—52	102	M, V
	"	VIII -64		18—44	85	M (T 62)
	"	VIII -66		18—52	147	M (T 48)
	"	VIII -67		18—27	40	T
		VII—X -59		18—52	239	V
21	Purkijaure	L IX -61		18—47	246	M, V
	"	IX -66		18—42	47	T
	"	VIII -67		18—30	40	T
		V—VIII -59		18—53	285	V
22	Vaikijaure	L IX -61		20—40	199	M, V
	"	VII -66		20—35	36	T
23	Karats	L IX -63		18—45	174	M
24	Juognajaure	L VIII -63	C. pidschian	21—25	51	M
25	Norvijaure	L X -63		21—41	8	T
26	Pelnijaure	L X -63		20—41	11	T
27	Mattisudden	R V, X -63		23—32	27	T
28	Laxede, Storsand	R IX -63		22—32	30	T
29	Harads	R X -62		25—33	50	M
30	Vittjärv	R VIII -62		26—36	50	M
31	Heden	R VIII -63		ca 30	11	M

Table 1. Continued.

No. cf. Fig. 1	Locality	Habitat and month	Species of whitefish	Number of gill-rakers	No. of whitefish examined	Kind of investiga-tion
32	Sunderbyn	R X -64	C. albula		15	T
33	Kusträsket	L IX -62	C. albula		49	M
	„	VI—VIII -64	C. lavaretus		65	T
34	Labbas, Rappen	L II -62		21—33	24	M
35	Tjeggelvas	L -67		24—34	75	M
36	Kidträsket	L X -63	C. albula		24	T
37	Malåträsk	L VII -64		25—38	33	T
38	Abraure	L VIII -63			53	M
39	Hornavan	L XII -61		31—40	18	T
40	Storavan	L VII -58	C. peled		19	T
		XI -65	C. peled	45—50	39	M
41	Pålänge	S I -63	C. albula		80	M
42	Storöhamn	S X -62	C. albula		117	M
43	Lule archipelago	S X—XI -62		21—38	117	M
	„ —	VII -63		21—28	26	T
	„ —	VI -64		21—32	20	T
44	Storuman	L VIII—IX -61		18—49	188	M, V
45	Vojmsjön	L VII—IX -61		17—52	231	M, V
46	Malgomaj	L VII—X -61		18—45	204	M, V
	„	V, X -62		19—41	84	M (T 67)
47	Tåsjön	L VIII—X -61		25—48	204	M, V
	„	VIII -62		38—45	48	T
	„	XI -63		35—48	157	M (T 47)
	„	VIII -64		40—48	73	M (T 39)
48	Viskasjön	L VIII -66		38—41	5	M
49	Stavarsjön	L VIII -66		38—40	5	M
50	Härnösand	S IX -63		26—34	15	T
51	Flåsjön	L VIII—X -61		20—40	76	M, V
	„	XI -63		21—28	26	T
52	Valsjön	L I -64		35—39	15	T
53	Västergean	L I -64		28—35	15	T
54	Västra Silen	L XI -63		28—35	17	T
55	Ören	L XI -63		21—35	15	T
	„	V, XI -65	C. albula		36	T
	„	VI -66	C. albula		57	T
56	Assjön	L X -63		27—32	15	T
57	Madkroken	L X -63	C. albula C. pidschian	16—21	35	T
58	Flåren	L X -63	C. albula		30	T
59	Immeln	L XI -63		32—38	20	T
60	Falkenberg	S IX -64		24—39	16	T
61	Ringsjön	L I -65		34—43	15	T
			Number examined		6921	
			Number M		6176	
			„ V		4215	
			„ T		1620	

Triaenophorus crassus FOREL 1880

In whitefish only plerocercoids occur. In Europe the adult stage has been found in *Esox lucius* L.

The plerocercoid is about 1 mm in width. It can be up to 390 mm long, which much exceeds the length of 130 mm mentioned by MILLER (1952).

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The worm has a complete scolex with the same form as the adult stage, with an apical dish and four three-spined hooks. These, too, have a somewhat greater width, basal plate 245—360 μ, than that given by MILLER, *l.c.*

The plerocercoid in the flesh is enclosed in cysts. Sometimes in young whitefish (0+), it has been found naked in the flesh (*cf.* MILLER 1952). In older fishes this is rare. In these cases it may perhaps be a new infestation occuring so close to the time of investigation that the tissue of the fish does not yet show any reaction.

Of the cysts 67.2 per cent were found in the epaxial muscles between the head and the dorsal fin. In the peritoneum and on the pyloric coeca only a few cysts were found. The majority of the cysts, 54.6 per cent, were on the right side of the fish. The difference, 521 out of 955 cysts, is significant ($P < 0.05$).

The bionomy of *T. crassus* is described by MILLER, *l.c.* The adult worm becomes fully mature at the time of the host's spawn. When the eggs are emitted the whole worm leaves the host. From the middle of June to the end of July the pike is almost free from *T. crassus*.

Suitable first intermediate hosts for the procercoid can be *Cyclops bicuspidatus* FORB. *C. strenuus* FISHER (VIK 1959), *C. vicinus* ULJ. and *Diaptomus gracilis* SARS (MICHAJLOV 1962).

The plerocercoid has been found in all species of coregonids. (OLSSON 1893, NYSTRÖM 1863, BERGMAN 1923, ZSCHOKKE 1933, VIK 1959, BAUER 1959.) It has, furthermore, been found in *Salmo trutta* L. (VIK 1959) and *Salvelinus alpinus* L. (NYSTRÖM 1863).

In chars from Lake Rebnisjaure, examined in September 1963, 54 per cent were infested. Infested *Thymallus thymallus* L. were found in the Lule älv river at Porsi 1967.

In fish farms it was found in *Salmo salar* L., *S. fontinalis* MITCHILL, *S. trutta*, *S. alpinus* and *Salvelinus namaycush* WALBAUM in Kusträsk and Porjus on the Lule älv 1963—65.

In *Coregonus*, *T. crassus* was found in 46 out of 54 localities shown in Fig. 3. In all localities except three in the upper part of the Lule älv (8, 9, 11) pike is present and consequently one of the presequisilas for the existence of *Triaenophorus*.

Eubothrium salvelini SCHRANK 1790

Adult worms are usually found in the pyloric coecae and the intestines of the char. The procercoid can develop in *Cyclops*. Infestation of the final host can take place directly from ingestion of infested copepods but also via an intermediate host, perch or stickleback. *E. salvelini* is unusual in whitefish (VIK 1963).

Only in one of the investigated lakes, Lake Flåsjön (51), were whitefish

Fig. 3. The distribution of *Triaenophorus crassus* •. Investigated localities without infested whitefish ○.

infested. Three out of 92 specimens (3.3 per cent) were found to harbour
E. salvelini in the intestines. The infested fishes were only 16—21 cm in
length; the infestation must therefore have been direct, as such small speci-
mens hardly eat fish.

Whitefish seem not to be a normal host. Transport of a frequent parasite,
from a fish species which is numerous, to a secondary host is common
(DOGIEL *et.al.* 1961).

Cyathocephalus truncatus PALLAS 1781

The larval stage of *C. truncatus* is found in the coelom of *Gammarus*. The
adult worm is localized to the pyloric coecae in *Salmonidae*. *C. truncatus*
has a wide distribution over the northern hemisphere. In Sweden the species
has been reported from whitefish in some lakes in central Sweden by OLSSON
(1893) and from char in the northern part of the country by BRINCK (1945).

The present investigation shows that the species is concentrated in the
northern part of Sweden (Fig. 4). Especially in the Lilla Lule älv river it
is frequent, while it seems to be lacking in the Stora Lule älv. *C. truncatus*
is most common in *Coregonus pidschian,* which is rare in the south of
Sweden.

Diphyllobothrium dendriticum NITZSCH 1824

The taxonomy of the genus *Diphyllobothrium* is very doubtful. Identi-
fication of the plerocercoids has been done according to KUHLOW (1953 a, b)
and WIKGREN 1964), whose nomenclature is followed.

The larvae are encysted on the stomach. The longitudinal subcuticular
muscle fibres are arranged in a single layer. Transverse sections almost
always have rounded margins. In tap water the larvae are immobile within
1—1.5 hours.

The procercoid is found in *Diaptomus* and *Cyclops*. The adult stage is
found in *Larus argentatus* BRÜNN, *L. canus* L., *L. ridibundus* L., *Rissa tridac-
tyla* L. and *Sterna hirundo* L.

The plerocercoid is reported from *Salmo trutta, Gaterosteus aculeatus* and
G. pungitius (KUHLOW 1953 b). WIKGREN (1964) has found it in *Coregonus
lavaretus* and *C. albula*.

Finds from earlier investigations in Sweden that can without doubt be
identified as *D. dendriticum* do not exist. LÖNNBERG (1892), OLSSON (1893),
BERGMANN (1923) and BRINCK (1945) reports cysts in the coelom in *Salve-
linus alpinus, Thymallus thymallus, Coregonus lavaretus, C. albula* and
Salmo irideus.

In Fig. 5 the finds from this investigation are shown. *D. dendriticum* has
been found in only four lakes.

Fig. 4. The distribution of *Cyathoce-phalus truncatus* ●. Investigated loca-lities without infested whitefish ○.

Fig. 5. The distribution of *Diphyllobothrium osmeri* ● and *D. dendriticum* ✳. Investigated localities without infested whitefish ○.
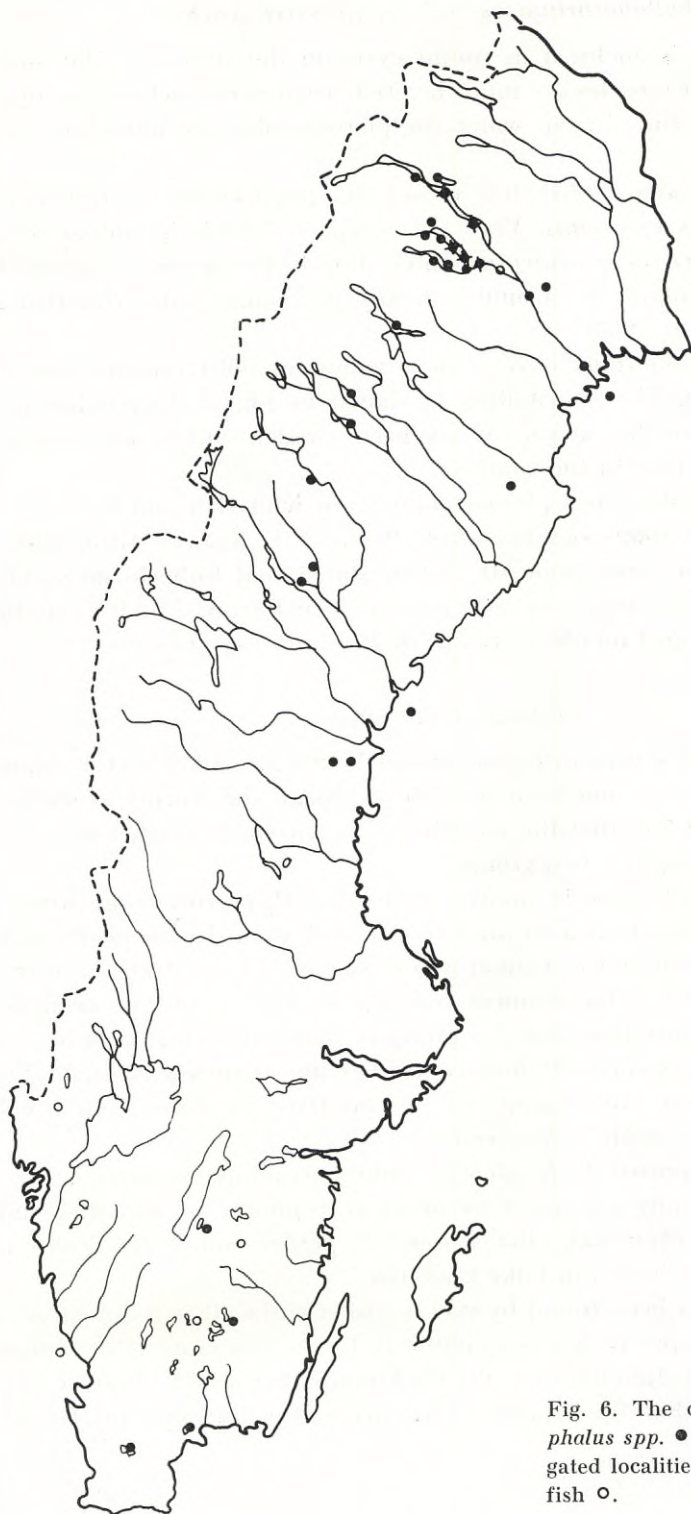
Fig. 6. The distribution of *Proteoce-phalus spp.* ● and *P. percae* *. Investigated localities without infested whitefish ○.

Diphyllobothrium osmeri (v. Linstow 1878)

The plerocercoid is enclosed in round cysts on the stomach. The longitudinal, subcuticular muscles are multi-layered. Transverse sections are often quadrangular in outline. In tap water the plerocercoids are immobile after about 5 minutes.

In Finland Wikgren (1964) has found the plerocercoid in *Coregonus albula* and *Osmerus eperlanus*. Vik (1964) reported finds in *Salmo salar, S. alpinus* and *Gasterosteus aculeatus*. Infestation in the genus *Coregonus* in Scandinavia and Finland is encountered only in vendace and whitefish in Lake Enare (Bylund 1966).

In this investigation finds have been common in both vendace and all species of whitefish. The distribution is shown in Fig. 5. Infestation is a regular occurrence in the interior of northern Sweden, but is less common near the coast, and rare in the south.

Lönnberg (1892) described plerocercoids from whitefish and vendace as *D. latum* (cf. Järvi 1909, Jääskeläinen 1915, 1921, Kajava 1913, Odenwall 1930). Wikgren and Muroma (1956) stated that hitherto no certain finds of *D. latum* in *Coregonus* had been reported from Finland. In the whitefish now examined no plerocercoids of *D. latum* were observed.

Proteocephalus spp

The taxonomy of the genus *Proteocephalus* Weinland 1858 is very doubtful. In most cases it has not been possible to assign the worms to species, largely owing to the fact that the whitefish was frozen. Nevertheless, it has been possible to distinguish two groups.

Proteocephalus sp I agree in many details with *P. percae*. Some worms, classed as I, were fixed in heated inert formol and stained with heametoxylineosin. Most of these had a distinct apical sucker, 53—58 testes, a cirrus pouch reaching to 1/3 of the segment, and the number of uterine branches was 7—9. It is therefore true that this group is identical with *P. percae*.

Proteocephalus sp II is like *P. longicollis*. The apical sucker is small. The number of testes is 75—100. Among the worms fixed as above some specimens certainly agreed with *P. longicollis*.

Olsson (1893) reported *P. longicollis* from *Coregonus lavaretus* and *C. albula*. This is the only statement as to *Proteocephalus* in whitefish and vendace in Sweden. Zschokke (1933) found *P. percae* and *P. longicollis* in the four species of whitefish in Lake Bodensee.

Proteocephalus has been found by me in whitefish in all parts of Sweden (Fig. 6). Certainly *P. percae* has been found in Lakes Lulejaure (13), Langas (12), Parkijaure (19), Randijaure (20), Purkijaure (21) and Vaikijaure (22) and *P. longicollis* in Randijaure and Vaikijaure and at the coast off Härnösand (50).

Table 2. Other parasites encountered besides Cestoda.

Species	Position of parasites	Locality (*cf.* Figs. 1 and 2)
Protozoa		
Henneguya zschokkei (GURLEY 1894)	Flesh	1, 7, 12, 13, 18—31, 41—43, 34, 36, 39, 44—47, 51, 54, 58
Trematoda		
Diplostomum spathaceum (RUD. 1819)	Eyelens	12, 13, 14, 23, 24, 26, 27, 28, 31, 33, 43, 46, 47, 50, 51, 52, 53, 54, 56, 57
Diplostomulum clavatum (NORDMANN 1832)	Vitreous body	12, 13, 23, 26, 27, 46, 47, 51, 57
Tetracotyle intermedia (HUGHES 1928)	Heart	7, 12, 13, 27, 28, 32, 43, 50, 52, 53, 55, 61
Crepidistomum farionis (MÜLLER 1874)	Intestine	12, 13, 21
Phyllodistomum conostomum (OLSSON 1876)	Gall bladder	7, 12, 13, 21, 22, 27, 28, 46
Nematoda		
Cystidicola farionis (FISCHER 1798)	Swimbladder	41—43, 50, 54
Rhaphidascaris acus (BLOCH 1779)	Cysts on stomach	All localities investigated
Camallanus lacustris (ZOEGA 1776)	Intestines	58
Gen. sp.	Intestines	
Acanthocephala		
Acanthocephalus lucii (MÜLLER 1776)	Intestines	12, 13, 20—22, 25, 43, 44, 50, 54
Echinorhynchus clavula (DUJARDIN 1845)	Intestines	12, 13, 20—22
E. truttae (SCHRANK 1788)	Intestines	26
Hirudinea		
Acanthobdella peledina (GRUBE 1851)	Dorsal fin	1, 22
Crustacea		
Argulus coregoni (THORELL 1864)	Skin, gills	22
Ergasilus sieboldi (NORDMANN 1832)	Gills	57, 58, 59
Salmincola salmonea (GISLER 1751)	Gills	43
S. alpina (OLSSON 1877)	Fins, gill-cover	12, 39, 46, 51
S. thymalli (KESSLER 1868)	Fins, gill-cover	27
Achteres coregoni (KESSLER 1868)	Fins	13, 27, 28, 46, 47

Other parasites

Besides the Cestoda mentioned above, many other parasites of no direct interest to this investigation were noted. They are listed in Table 2.

V. Feeding habits of whitefish

The feeding habits of whitefish are of essential importance as regards parasite invasion, and therefore a short summary of these habits will be given here.
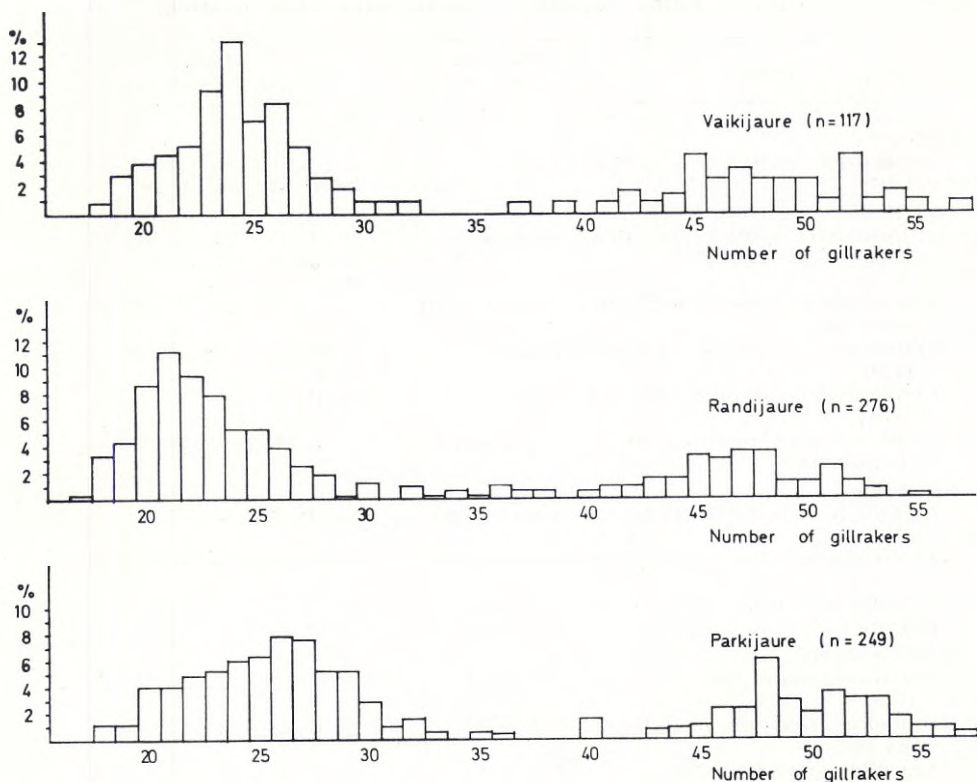
Fig. 7. Whitefish populations from Lakes Vaikijaure, Randijaure and Parkijaure; number of gillrakers in per cent.

Food competition between *Coregonus pidschian* and *C. peled* in Lake Vojmsjön was examined by NILSSON (1958), who found that the smaller specimens of *C. peled* fed mainly on *Entomostraca,* while *C. pidschian* fed predominantly on bottom animals. Furthermore NILSSON (1960) studied food in *C. pidschian, lavaretus* and *peled* in Lakes Storavan and Uddjaur. The predominating food was as follows: in *C. pidschian,* bottom animals during the whole year; in *C. peled,* emerging or winged insects in summer, *Entomostraca* in autumn and winter; in *C. lavaretus, Cladocera* in July—December.

Certain lakes in the Lilla Lule älv river system — Vaikijaure, Randijaure, and Parkijaure (22, 20, 19) — were examined in greater detail as regards the food selection of the whitefish.

The material was treated according to NILSSON (1957), with the exception that the amount of food was weighed and not calculated on a volume basis. Thus, for each food group the percentage of weight was calculated for each
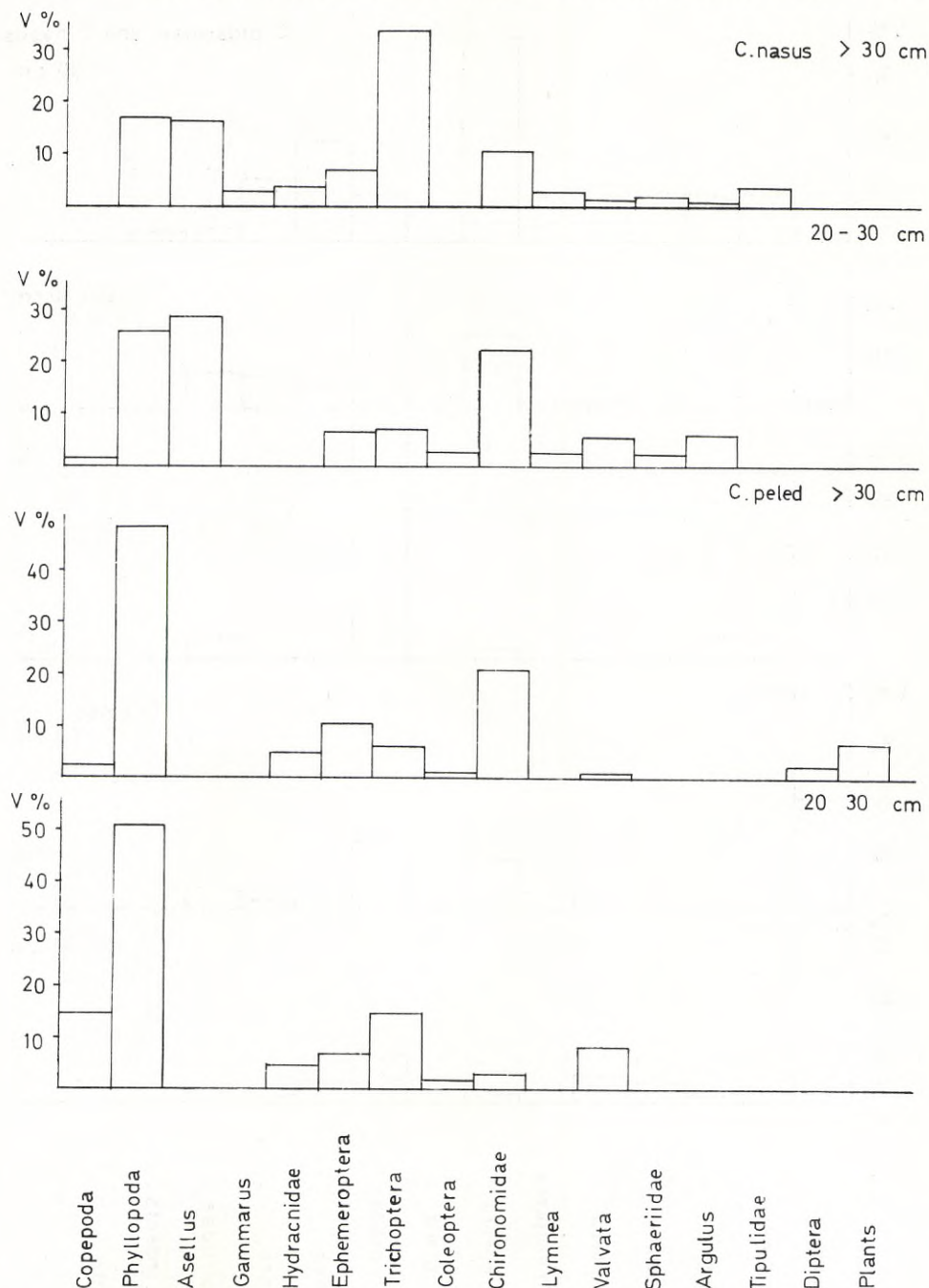
Fig. 8. The feeding habits of whitefish in Lake Vaikijaure during June, August and September 1959.

V %=Sum of the percentage (weight) of every food item divided by the number of stomachs.
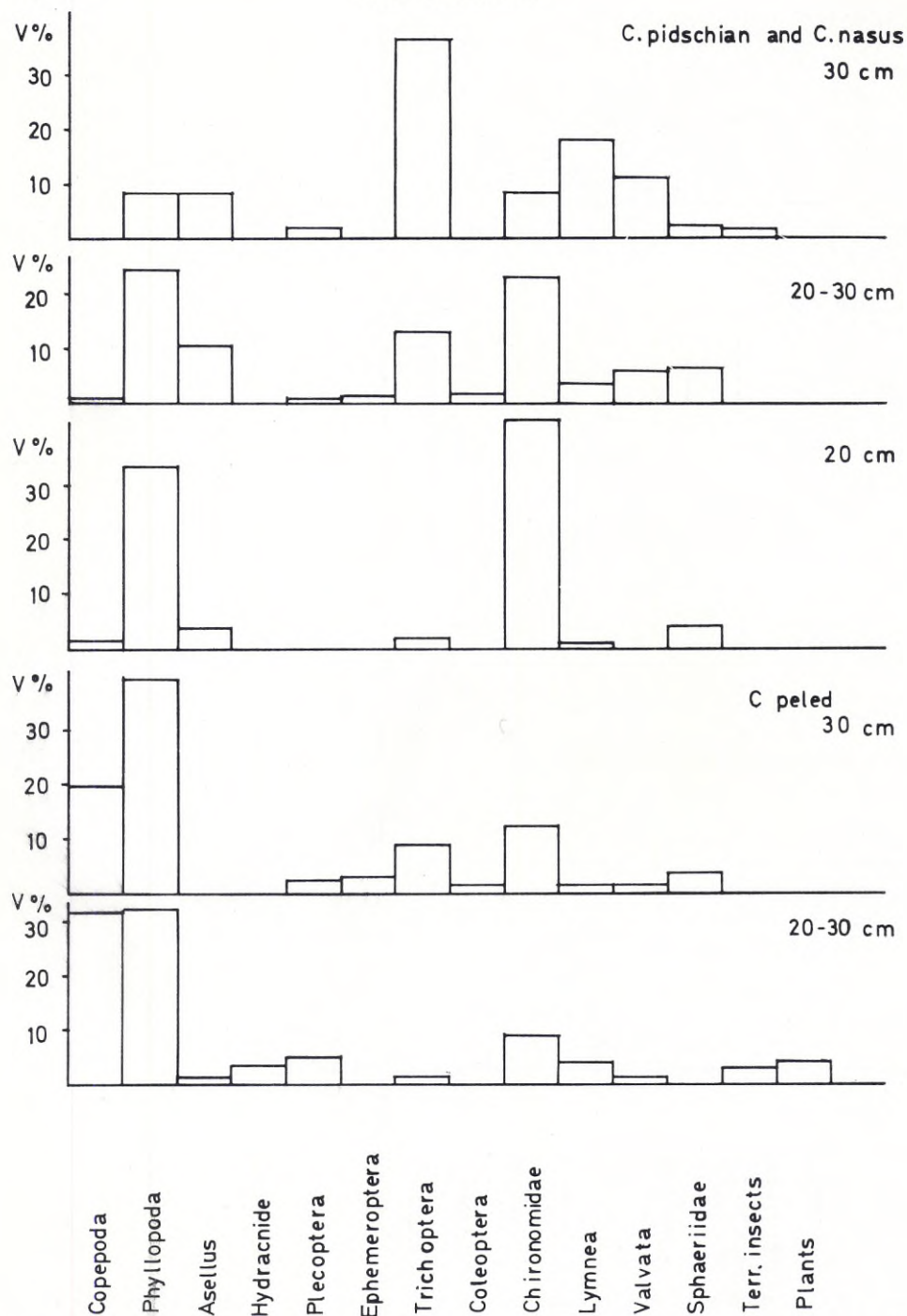
Fig. 9. The feeding habits of whitefish in Lake Randijaure during July, August and October 1959
Abbreviations, see Fig. 8.
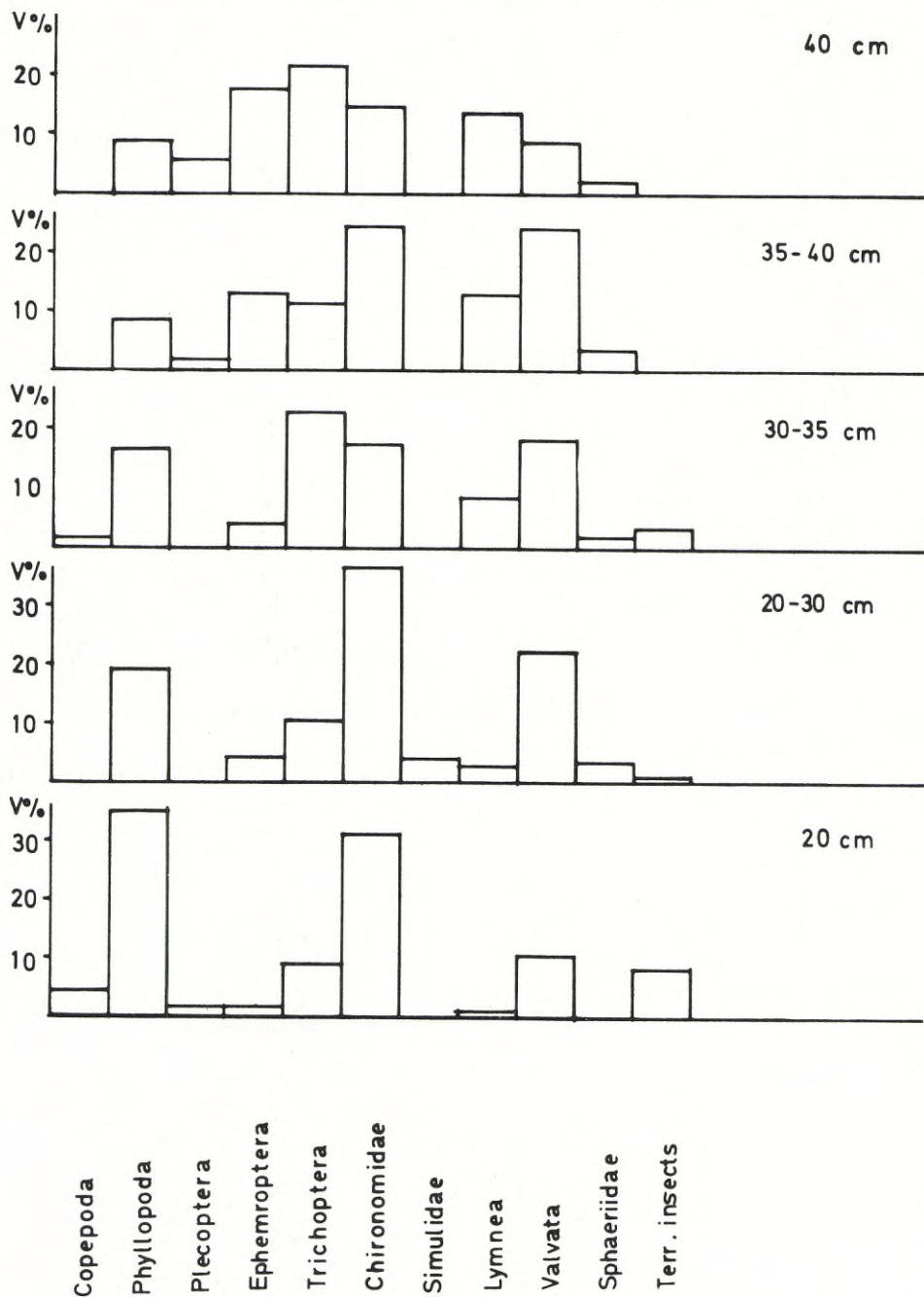
Fig. 10. The feeding habits of *Coregonus pidschian* and *C. nasus* in Lake Parkijaure during June, July, August and October 1959.
Abbreviations, see Fig. 8.
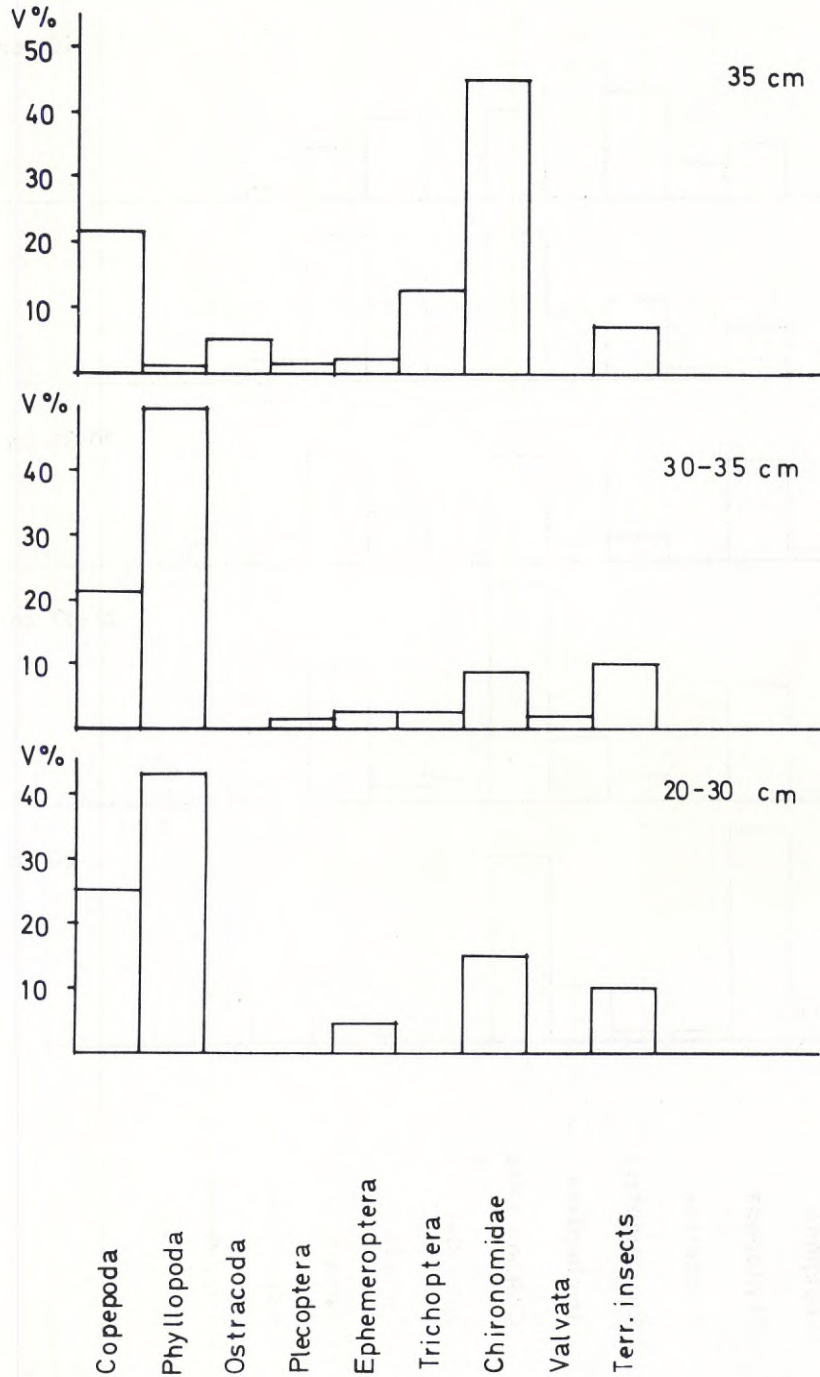
Fig. 11. The feeding habits of *Coregonus peled* in Lake Parkijaure during June, July,
August and October 1959.
Abbreviations, see Fig. 8.
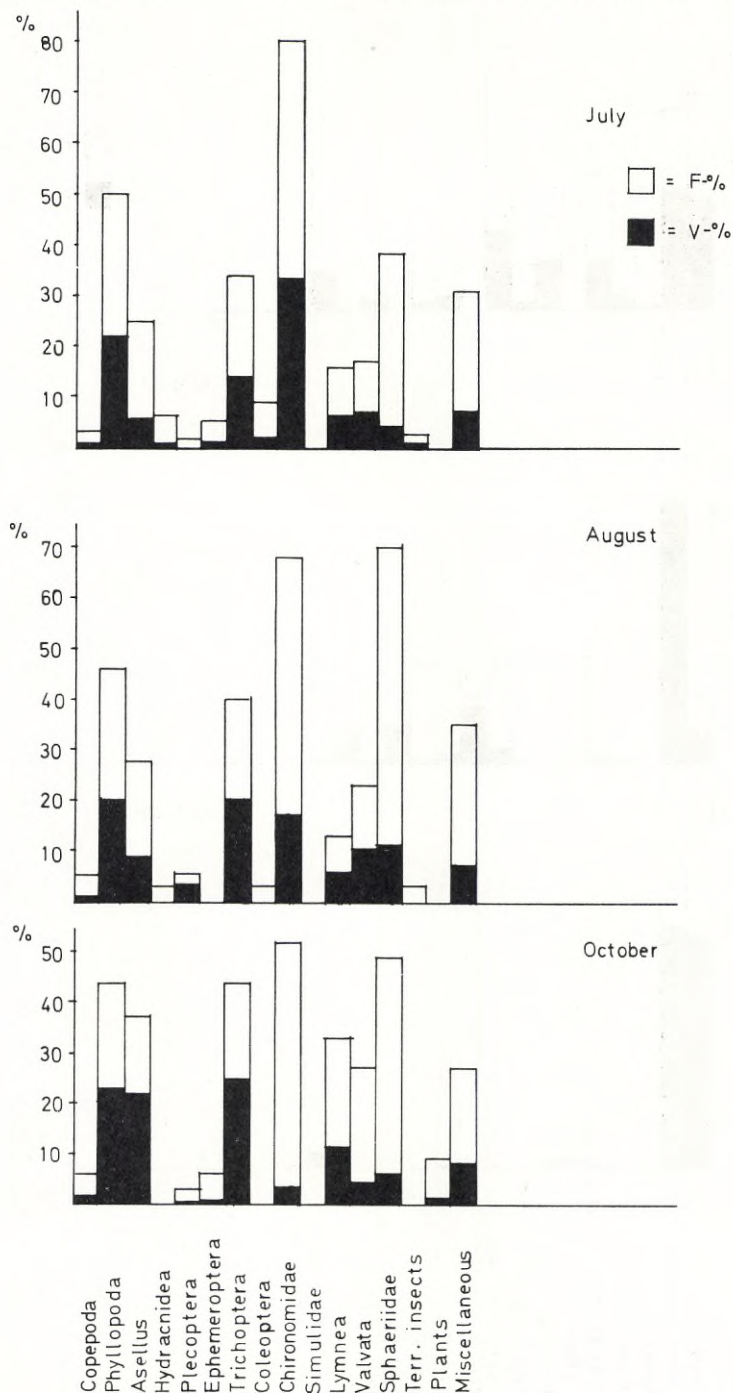
Fig. 12. The feeding habits of *Coregonus pidschian* and *C. nasus* in Lake Randijaure during separate months.

F %=Frequency of the food item. V %, see Fig. 8.
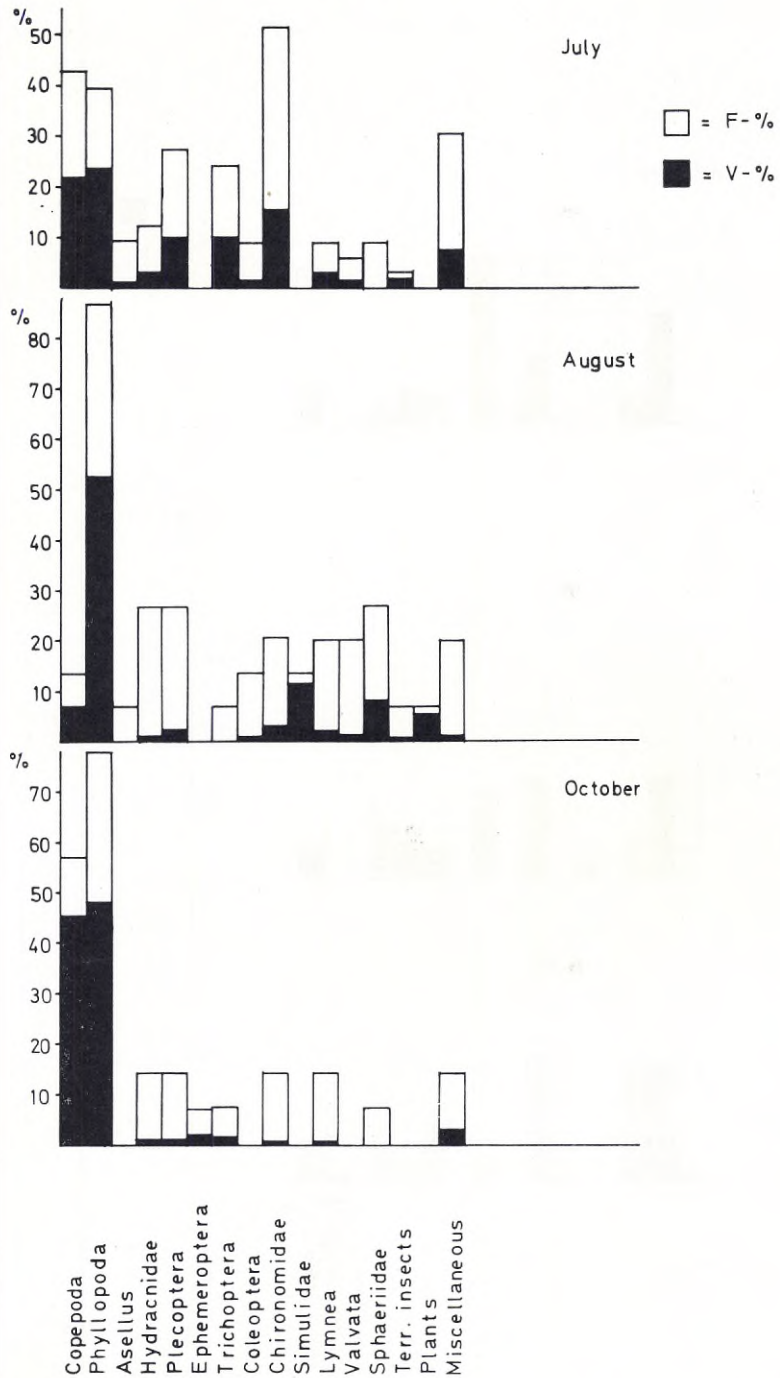
Fig. 13. The feeding habits of *Coregonus peled* in Lake Randijaure during separate months. Abbreviations, see Fig. 12.
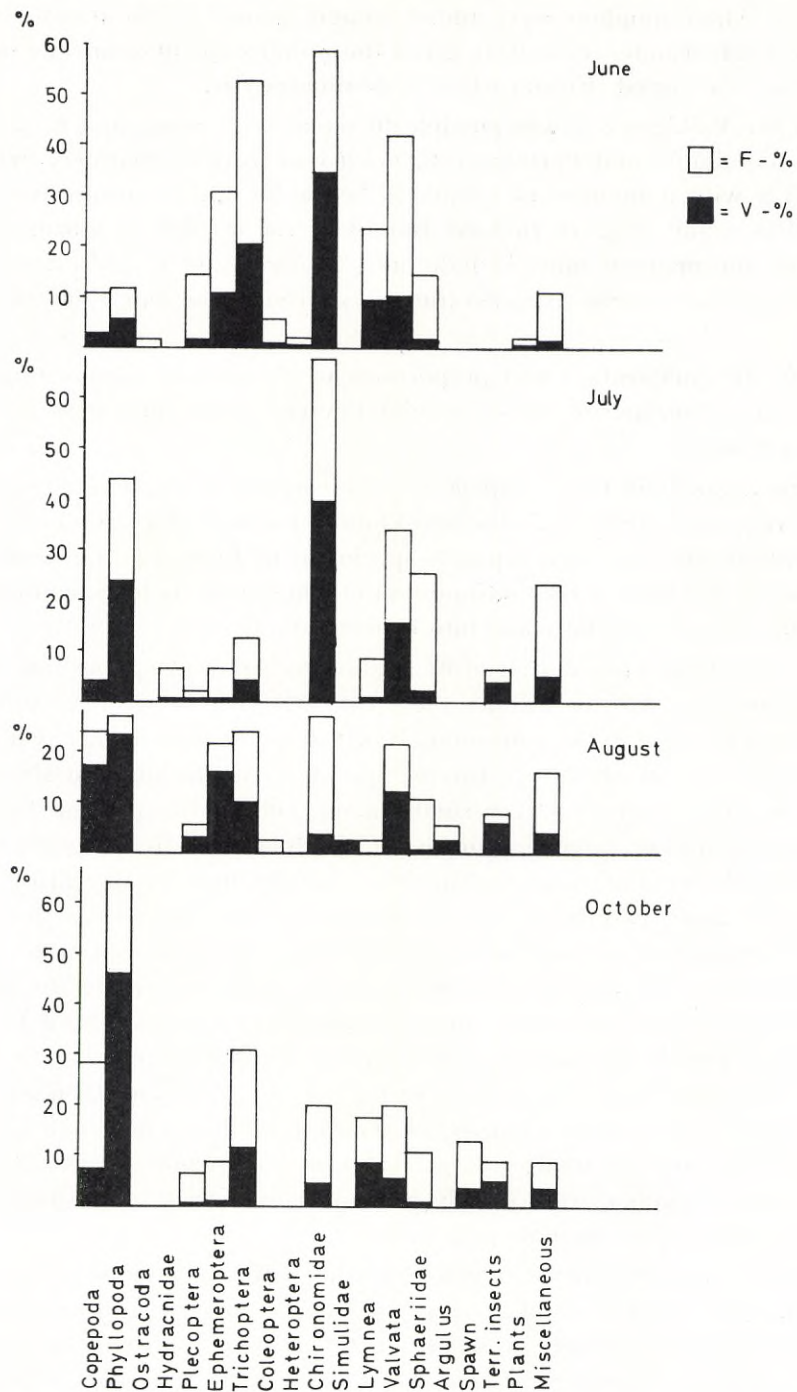
Fig. 14. The feeding habits of whitefish in Lake Parkijaure during separate months. Abbreviations, see Fig. 12.

stomach. These numbers were added up and divided by the number of sto-
machs. Furthermore, there were given the proportions of stomachs where a
food item was found (F) and where it dominates (D).

In Lake Vaikijaure it was possible to separate *C. nasus* and *C. peled*. In
Lakes Randijaure and Parkijaure *C. peled* was treated separately, while all
whitefish with a number of gillrakers below 29 and 31 respectively were
treated as a unit (Fig. 7). In Lake Randijaur the number of gillrakers is so
low that the material must include both *C. nasus* and *C. pidschian*. When
processing the material, consideration was given to the length of the white-
fish.

As to the composition and proportions of the Cestode fauna, *Copepoda,
Asellus* and *Gammarus* are of special interest, since they serve as inter-
mediate hosts.

In the majority of cases, *Copepoda* — in contrast to *Phyllopoda* — consti-
tute a very small part of all the planktons consumed (Figs. 8—11). It must
be assumed, however, that separate specimens of *Copepoda* are likely to be
included in the food, if the consumption of *Phyllopoda* is high; consequently
the latter should also be taken into consideration.

A study of the choice of food in relation to different species and groups
of different sizes reveals at once the great difference between *C. pidschian-
nasus* and *C. peled* in the consumption of *Copepoda*. The former had hardly
eaten *Copepoda* at all, except for the specimens in the smallest size group,
and even there only to a very small extent. On the other hand, *Copepoda*
constitute a rather large proportion of the total food in *C. peled* and —
except in the case of Lake Vaikijaure — invary little in the different size
groups. In Lake Vaikijaure only *C. peled* of a size lesser than 30 cm had
eaten *Copepoda* to an extent worth mentioning. The consumption of *Phyllo-
poda* decreases as the fish size increases. In Lake Parkijaure the smallest
C. pidschian-nasus have eaten more *Phyllopoda* than the biggest *C. peled,*
but that is not the case in Lakes Randijaure and Vaikijaure. It was only in
Lake Vaikijaure that *Gammarus* was part of the food, and then merely in
C. nasus of a size bigger than 30 cm. *Trichoptera* and *Chironomidae* domi-
nate in the choice of food of *C. pidschian-nasus. Asellus,* intermediate host
for *Achanthocephala,* were mainly consumed by rather large specimens of
whitefish with a low number of gillrakers.

The composition of the food chosen during different periods is reported in
Figs. 12—14. *Copepoda* and *Phyllopoda* show an increase towards late sum-
mer and autumn, as well as *Asellus* in *C. pidschian-nasus* in Lake Randi-
jaure. In early summer *Chironomidae* form a very large part of the food
consumed, but towards autumn a marked decrease was noticed. The part
of *Mollusca* remains relatively constant throughout the season.

VI. Frequency of *Cestoda* in different species of whitefish

Below will be treated the material from a number of localities which have been more thoroughly investigated.

A. *Triaenophorus crassus*

a. Lilla Lule älv river (Fig. 2)

Vaikijaure (22)

Lake Vaikijaure is situated 258 m above sea level, and is about 7 km long and 5 km broad with an area of 23.1 km². Within large zones the lake is very shallow, about 3 m. The shores are flat. The stock of fish according to test fishing is composed of: trout (less than 0.1 %), grayling 2.6 %, whitefish 57.7 %, pike 6.6 %, perch 26.9 %, roach 5.7 % and burbot 0.5 %. These numbers say little about the real composition of fish species, but will be of guidance when the relative differences between different lakes are to be estimated.

The composition of the stock of whitefish is such that it cannot be divided into particular species (Fig. 7). Whitefish occur with all numbers of gill-rakers from 17 to 55, but specimens with more than 40 gillrakers are rare and unfortunately are not represented in the material examined for parasites. There is a small peak for specimens with about 32 gillrakers, which represent a dwarf form of *C. lavaretus* — mature — when it is only 15 cm long.

The frequency of whitefish infested by *Triaenophorus crassus* is reported in Table 3, and the choice of food in the material examined for parasites is shown in Table 4.

Purkijaure (21)

This lake is 272 m above sea level, and is about 8 km long and 8 km broad with an area of 20.2 km². Within large zones the lake is very shallow, but in the western parts it is deeper.

Stock of fish: trout 0.1 %, grayling 1.5 %, whitefish 49.4 %, pike 2.6 %, perch 14.5 %, roach 31.9 %, burbot and ide.

Here, too, whitefish with a low number of gillrakers predominate. The composition of the population is reported in Fig. 15. Here the distribution is more balanced: *C. pidschian* dominates slightly, *C. lavaretus* show no dwarf forms, *C. peled* is less frequent than in Lake Vaikijaure.

The invasion of *Triaenophorus* is reported in Table 3, and the choice of food in the material examined for parasites in Table 5.

Randijaure (20)

The lake is situated 283 m above sea level, and is 13 km long and 6 km broad with an area of 51.1 km². The southern part of the lake is shallow within large areas, it has slightly sloping shores, which are partly cultivated. Stock of fish: trout 0.2 %, grayling 4.2 %, whitefish 43.2 %, pike 2 %, perch 50.1 %, roach 0.2 %, burbot 0.4 %.

Table 3. Infestation by *Triaenophorus crassus* in

Locality		Number of											
		17	18	19	20	21	22	23	24	25	26	27	28	29
Vaikijaure (22) 1961, IX	No. examined	—	—	—	4	8	16	29	18	18	13	14	11	8
	„ infested	—	—	—	1	1	2	2	2	2	2	2	1	1
	% infested							11.5						
	No. of worms/inf.							1.1						
1967, X	No. examined	—	—	—	—	2	2	11	6	4	6	7	3	2
	„ infested	—	—	—	—	—	—	—	1	—	—	2	2	—
	% „							11.6						
Purkijaure (21) 1961	No. examined	—	1	9	15	25	13	12	18	10	17	18	20	8
	„ infested	—	—	1	2	3	1	2	—	1	—	1	2	1
	% „							8.4						
	No. of worms/inf.							1.3						
1967	No. examined	—	4	10	39	26	24	20	16	13	11	15	14	6
	„ infested	—	—	—	6	3	2	2	3	2	1	—	2	—
	% „							10.6						
Randijaure (20) 1961	No. examined	—	1	6	15	16	18	10	6	3	1	4	1	—
	„ infested	—	—	—	3	1	4	1	1	1	—	—	—	—
	% „							13.6						
	No. of worms/inf.							1.2						
1966 (central part)	No. examined							25						
	% infested							16.0						
1966 (rapid Parki)	No. examined							47						
	% infested							29.1						
Parkijaure (19) 1966	No. examined	—	2	5	5	2	6	6	4	1	1	6	5	5
	„ infested	—	1	3	4	1	3	1	1	1	1	2	3	2
	% „							51.0						
	No. of worms/inf.							1.3						
Skalka (18) 1961	No. examined	—	1	—	—	1	1	3	—	—	1	2	1	1
	„ infested	—	—	—	—	—	1	—	—	—	1	—	1	—
	% „							33.3						
	No. of worms/inf.							1.5						
Tjåmotisjaure (17) 1961	No. examined	2	2	11	6	39	16	14	2	22	4	1	1	2
	„ infested	—	1	3	1	8	6	4	2	1	1	—	1	—
	% „							27.6						

The composition of the population of whitefish is reported in Fig. 7. The number of *C. peled* is greater than in the lakes downstream. Hybridization has occurred to a great extent and whitefish with all numbers of gillrakers from 17 to 55 have been found.

The frequency of *Triaenophorus crassus* is reported in Table 3, and choice of food in Table 6.

Parkijaure (19)

The lake is situated 292 m above sea level, and is 10 km long and 3 km broad with an area of 18.6 km². It is deep and has steeply sloping stony shores. Stock of fish: trout 0.2 %, grayling 1.6 %, whitefish 49.1 %, pike 3.9 %, perch 45.2 %, roach and burbot.

whitefish in lakes from Lilla Lule älv river system.

gillrakers

30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	Total
16	13	12	8	6	1	2	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	199
7	3	7	3	3	1	1	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	43
							45.0																		
							1.5																		21.6
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	43
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5
																									11.6
14	19	11	12	5	3	3	4	1	—	2	—	1	2	—	—	—	3	—	—	—	—	—	—	—	246
3	2	1	3	2	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	28
							17.5																		
							1.2																		11.5
22	15	9	13	5	10	—	6	1	3	2	—	—	—	1	—	—	—	—	—	—	—	—	—	—	285
3	2	1	2	1	1	—	2	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	35
							16.1																		12.3
—	—	—	1	1	2	1	1	—	—	1	—	—	—	1	1	3	2	1	2	1	—	2	—	—	101
—	—	—	1	1	2	1	1	—	—	1	—	—	—	1	—	2	—	1	1	1	—	1	—	—	21
							50.0																		
							1.4																		20.8
—	—	—	—	—	—	—	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	37
							58.3																		29.7
—	—	—	—	—	—	—	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	62
							33.3																		30.7
—	3	1	—	1	—	—	—	—	—	—	1	—	—	1	1	2	4	3	2	1	1	2	—	1	72
—	3	—	—	1	—	—	—	—	—	—	1	—	—	1	1	2	3	3	2	1	1	2	—	1	45
														94.7										
														1.7										62.5
—	—	—	1	—	—	1	—	—	—	—	1	3	3	2	6	9	15	14	9	10	4	13	4	2	108
—	—	—	1	—	—	1	—	—	—	—	1	2	1	—	4	6	10	10	7	7	3	12	2	2	72
														70.8										
														1.8										66.7
—	—	—	—	—	1	2	2	4	2	—	—	—	—	—	—	—	—	—	1	—	1	1	1	—	117
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	40
																									34.2

The composition of the stock of whitefish is reported in Fig. 7. *C. peled* is here rather obviously different from *C. pidschian* — *C. nasus*; it is also more frequent. For the frequency of *Triaenophorus*, see Table 3.

Skalka (18)

The lake is 295 m above sea level, and is 26 km long and 2 km broad with an area of 46.4 km^2. Its characteristics are similar to these of Lake Parkijaure. Stock of fish: trout 0.2 %, grayling 4.0 %, whitefish 49.3 %, pike 5.5 %, perch 41.0 %, roach and burbot.

The composition of the population of whitefish is reported in Fig. 16. The rate of plankton-eating whitefish is about the same as in Lake Parkijaure. For the frequency of *Triaenophorus*, see Table 3. The choice of food in the material examined for parasites is reported in Table 7.

Table 4. The feeding habits of whitefish in Lake Vaikijaure during September. gr=number of gillrakers, F %=frequency of the food item, D %= dominating food item, percentage of total number examined whitefish.

	F-%		D-%	
	20—29 gr	30—40 gr	20—29 gr	30—40 gr
Eurycercus	14.0	63.6	14.0	63.6
Asellus	34.0	45.5	28.0	18.2
Chironomidae	8.0	—	2.0	—
Trichoptera	22.0	—	14.0	—
Sphaeriidae	48.0	18.2	28.0	18.2
Lymnea	10.0	18.2	2.0	—
Valvata	10.0	—	6.0	—
Gyraulus	6.0	—	6.0	—
Algae	6.0	18.2	—	—
Empty	32.4	62.1	—	—
Number examined	139	60	—	—
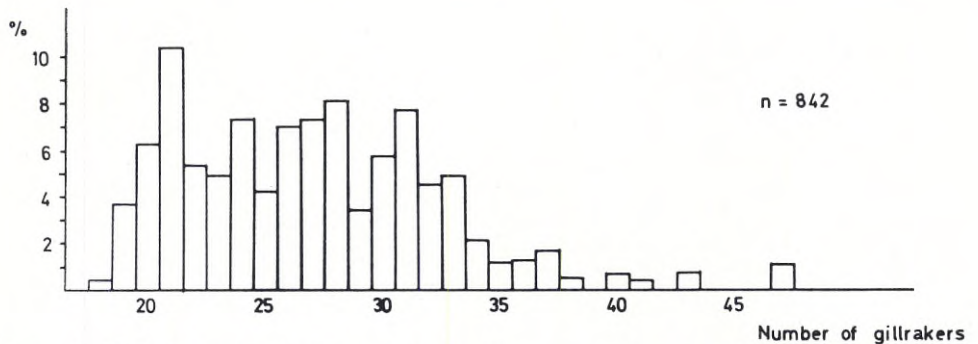
Fig. 15. Whitefish populations in Lake Purkijaure; number of gillrakers in per cent.

Table 5. The feeding habits of whitefish in Lake Purkijaure during September and October.
Abbreviations, see Table 4.

	F-%		D-%	
	20—29 gr	30—40 gr	20—29 gr	30—40 gr
Cyclops	—	2.5	—	-
Bosmina	2.5	12.5	2.5	10.0
Eurycercus	45.0	20.0	41.3	20.0
Gammarus	1.3	—	—	—
Asellus	33.8	45.0	26.3	40.0
Chironomidae	5.0	7.5	5.0	2.5
Trichoptera	25.0	20.0	21.3	17.5
Ephemeroptera	1.3	5.0	—	5.0
Corixa	1.3	2.5	—	—
Sphaeriidae	6.3	7.5	2.5	5.0
Valvata	1.3	2.5	1.3	—
Algae	7.5	—	—	—
Empty	36.0	38.5	—	—
Number examined	166	80	—	—

Table 6. The feeding habits of whitefish in Lake Randijaure during September and October.
Abbreviations, see Table 4.

	F-%		D-%	
	18—28 gr	33—52 gr	18—28 gr	33—52 gr
Bosmina	4.9	75.0	2.4	75.0
Eurycercus	24.4	12.5	—	12.5
Asellus	22.0	—	22.0	—
Chironomidae	24.4	—	14.6	—
Trichoptera	19.2	12.5	14.6	—
Ephemeroptera	2.4	—	2.4	—
Hydracnidae	4.9	—	—	—
Sphaeriidae	14.6	—	—	—
Lymnea	2.4	—	—	—
Valvata	19.5	—	12.2	—
Gyraulus	7.3	—	4.9	—
Terrest. insects	—	12.5	—	12.5
Algae	2.4	—	2.4	—
Empty	46.8	55.6	—	—
Number examined	81	20	—	—

Tjåmotisjaure (17)

The lake is 297 m above sea level, and is 15 km long and 2 km broad with an area of 13.4 km². Its characteristics are the same as for Lake Skalka. In the eastern part it is connected with Lake Jäkkaure by the Blackälv River. Stock of fish as represented by test fishing with net: trout 0.8 %, grayling 5.0 %, whitefish 66.7 %, pike 3.1 %, perch 24.4 %, roach > 0.1 %, burbot > 0.1 %.

As will be seen in Fig. 17, there is a marked division of the stock of whitefish into two populations: one consists almost purely of C. peled, the other is more composite.

The invasion of T. crassus is reported in Table 3.
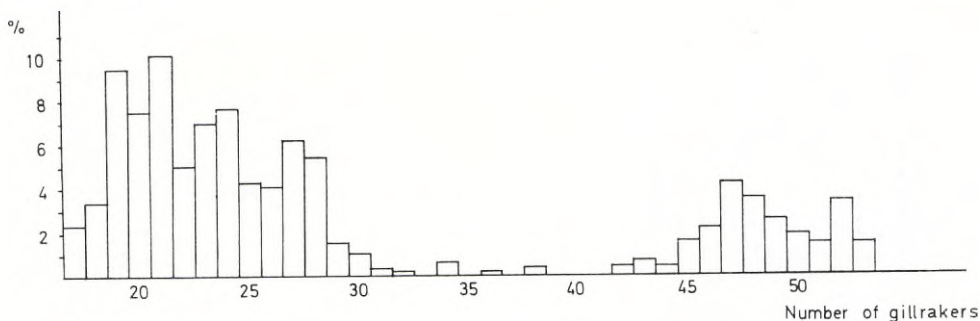
Fig. 16. Whitefish populations in Lake Skalka; number of gillrakers in per cent.

Table 7. The feeding habits of whitefish in Lake Skalka during September. Abbreviations, see Table 4.

	F-%		D-%	
	18—34 gr	35—54 gr	18—34 gr	35—54 gr
Copepoda	—	40.9	—	9.1
Cladocera	—	77.3	—	71.3
Chironomidae	33.3	6.1	33.3	4.6
Trichoptera	33.3	1.5	33.3	1.5
Ephemeridae	—	1.5	—	1.5
Valvata	33.3	—	33.3	—
Hydracarina	—	1.5	—	—
Terrest. insects	—	9.1	—	9.1
Algae	—	3.0	—	3.0
Empty	50.0	18.5	—	—
Number examined	12	96	—	—

Jäkkaure (16)

Rather than a lake, this is a lakelet (area 2 km², formed by the River Blackälven, falling into Lake Tjåmotisjaure. The stock of whitefish is dominated by a small-size population of *C. pidschian* or *C. pidschian* — *C. nasus*; they are mature when they are only 15 cm long.

The material examined was caught during spawning time by means of gill-net fishing under ice in November 1966, and its average length was 17.2 cm. The average age was 5 years. The number of gillrakers varied between 17 and 25, with an average of 20.1. Out of 50 specimens examined, 15 (30.0 per cent) were infested with *T. crassus*.

Furthermore there were examined 25 *C. peled* from Lake Jäkkaure with an average of 48 gillrakers and an average length of 28 cm; 15 of them (57.5 per cent) were infested.
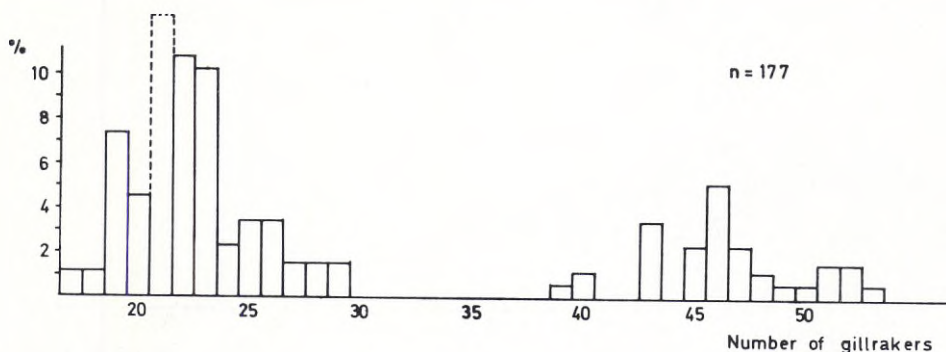
Fig. 17. Whitefish populations in Lake Tjåmotisjaure; number of gillrakers in per cent.

Table 8. Infestation by *Triaenophorus crassus* in whitefish in lakes from Lilla Lule älv river system (percentage).

	Whitefish with < 30 gr	Whitefish with > 30 gr	t-test	
Vaikijaure (1961, 66)	11.5	45.0	p < 0.001	t. 4.90
Purkijaure (1961, 67)	9.6	16.8	< 0.05	2.90
Randijaure (1961, 66)	13.6	50.0	< 0.01	4.95
Parkijaure (1966)	51.0	94.7	< 0.001	4.78
Skalka (1961)	33.0	70.8	< 0.05	2.60
Tjåmotis (1961)	27.6	80.0	< 0.001	4.68
Jäkkaure (1966)	30.0	57.5	< 0.05	2.35

Discussion

The frequency of whitefish infested with *T. crassus* differs very much in the various lakes.

To judge from fish tagging, carried out in Lake Randijaure, there is no communication — or in any case very little — between the populations of whitefish in the different lakes. Out of 340 specimens of whitefish, tagged in the south part of Lake Randijaure, 13.5 per cent were recaptured: all of them in this lake, and some of them in its northern part. The whitefish tagged were caught in seine-net fishing, the usual salmon smolt tags (type CARLIN) being used.

The results of test fishing show that the total share of whitefish in regard to the whole stock of fish seems to be about the same in all the lakes with the exception of Lake Jäkkaure. On the other hand, the composition of whitefish with different numbers of gillrakers differs in the various lakes. Whitefish with a great number of gillrakers, *C. peled,* constitute only a small part of the total population in the shallow Lakes Vaikijaure, Purkijaure and Randijaure. They are considerably more frequent in the deeper lakes upstream, where there also is a greater infestation with *T. crassus.*

In all lakes there is a great difference in infestation by *T. crassus* between whitefish with a large and with a low number of gillrakers. These differences were t-tested and found statistically significant for all lakes (Table 8).

The distinction between the groups is relatively constant in the different lakes. Thus, a large parasite invasion in *C. peled* implies a large invasion in *C. pidschian* — *C. nasus.* Only in Lake Vaikijaure does the regression coefficient diverge (Fig. 18). The regression coefficients are significant for all the lakes with the following values of P.

Vaikijaure: $0.01 > P > 0.001$
Purkijaure: $P < 0.001$
Randijaure: $0.01 > P > 0.001$
Skalka: $0.02 > P > 0.01$
Tjåmotis: $P < 0.001$
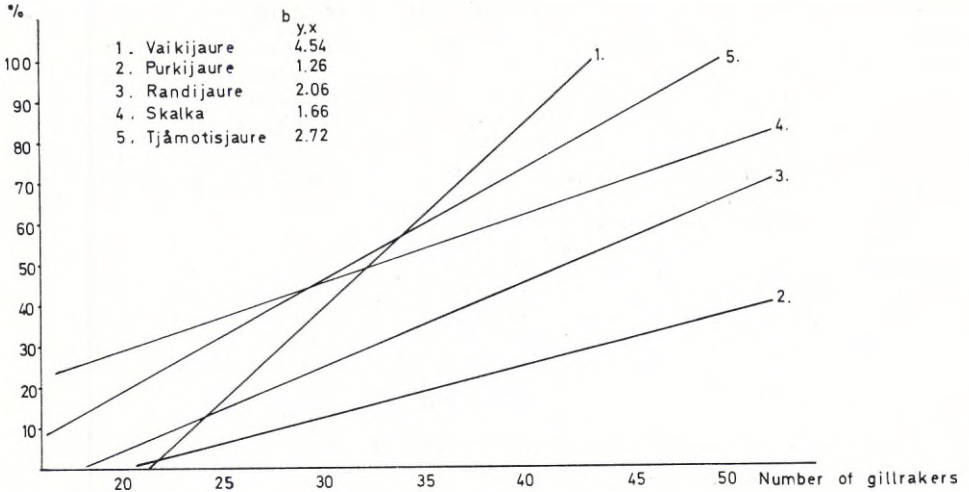
Fig. 18. Infestation by *Triaenophorus crassus* in whitefish in relation to number of gill-rakers in lakes in Lilla Lule älv river system.

The material represented in Table 3 was processed according to the number of gillrakers, and for each was calculated the percentage of infested whitefish. The calculation does not include cases where a certain number of gillrakers was represented by only one or two of the specimens examined.

A more extensive investigation in the feeding habits of whitefish in Lakes Vaikijaure, Randijaure and Purkijaure has been reported in the previous, *cf.* section 5. The consumption of *Copepoda* and *Phyllopoda* was about the same in the three lakes as regards *C. peled* in size group 20—30 cm (*cf.* Figs. 8—11). For whitefish of bigger size it should be noted that in Lake Parkijaure the food composition was — to the same extent — the same as above, while in Lake Vaikijaure there was some changing over to *Chironomidae* and, above all, the proportion of *Copepoda* in food had decreased. In Lake Randijaure there was also a decrease of *Copepoda* in comparison with Lake Parkijaure, but the percentage change was smaller. For *C. peled* the above seems to correspond very well to the differences in the *Triaenophorus* infestation: a very high frequency in Lake Parkijaure, a lower one in Lake Randijaure, and a still lower in Lake Vaikijaure.

In the more limited material examined for parasites it was only in Lake Skalka that whitefish with a high number of gillrakers fed on *Copepoda* (Table 4—7). The frequency of *Phyllopoda* was high in Lakes Randijaure and Vaikijaure but relatively low in Lake Purkijaure. Even these differences, which give only a momentaneous picture of the choice of food, were reflected in the frequency of infestation with *T. crassus*. The differences in parasite

Table 9. Infestation by *Triaenophorus crassus* in whitefish in Lakes Karats and Jougnajaure.

Locality		Number of gillrakers																									Total
		17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	
Karats (23)																											
Harrok	Number examined	1	—	1	—	7	8	10	9	8	1	7	2	2	2	3	1	—	5	2	2	3	—	—	1	—	73
	infested	—	—	—	—	2	2	3	5	2	—	1	1	1	—	—	—	—	2	1	1	2	—	—	1	—	23
	%							28.9												34.8							31.5
Karatsudden	Number examined	—	—	1	1	3	10	11	16	10	14	2	2	2	—	1	2	1	—	—	—	—	—	—	1	—	55
	infested	—	—	1	1	—	2	6	4	1	7	1	1	—	—	1	1	—	—	—	—	—	—	—	—	—	24
	%							32.9																			32.0
Kiddajaure	Number examined	—	—	1	—	1	5	4	3	4	—	2	1	—													21
	infested	—	—	—	—	1	—	1	—	—	2	1															2
	%							9.5																			9.5
Juognajaure (24)	Number examined	—	—	—	—	2	2	9	16	13	6	2	1														51
	infested	—	—	—	—	—	—	—	1	2	—	—	1														4
	%							7.8																			7.8

infection in the various lakes can consequently be explained by the differences in feeding habits.

For *C. pidschian* — *C. nasus* the consumption of *Copepoda* and *Phyllopoda* was considerably less than for whitefish with a high number of gillrakers. The general conditions in Lakes Vaikijaure, Randijaure and Parkijaure differ very little, and yet these lakes present great differences as to infestation with *Triaenophorus*. It is obvious that a high degree of infestation in whitefish with a high number of gillrakers may increase the total infection level, so long as that this species of whitefish constitutes an important part of the whole stock of whitefish. According to the results from test fishing, whitefish with more than 40 gillrakers constitute 5 per cent of the total whitefish stock in Lake Vaikijaure, and 2 per cent in Lake Purkijaure, while the percentage differs between 20 and 35 per cent in the upstream lakes; Lake Parkijaure has the highest percentage and also the highest degree of infestation.

b. River Pärlälven

Karats (23)

Lake Karats is situated 414 m above sea level with an area of 59.6 km², and though it flows the River Pärlälven, a tributary of the Lilla Lule älv river. The stock of fish according to test fishing is composed: trout 2.5 %, grayling 0.3 %, whitefish 56.3 %, pike 5.0 %, perch 33.6 %, burbot 1.4 %. The lake is about 150 m higher up than the other lakes mentioned, yet it has about the same composition of fish species.

In the lake, which has a length of 28 km, samples were drawn partly at Harrok in the middle of the lake, partly in the eastern part, Karatsudde, and partly in the shallow north-eastern part, Kiddajaure, which is practically cut off from the rest of the lake. The invasion of *T. crassus* is demonstrated in Table 9. The result does not indicate any difference between the two localities in the main lake, though they lie far apart, while the more isolated Kiddajaure shows a considerably lower frequency. It is of interest to note that there are hardly any whitefish with a high number of gillrakers here.

Juognajaure (24)

Lake Juognajaure is situated in the Pärlälven river, at 20 km from Lake Karats downstream. As in Kiddajaure, there are only whitefish with a low number of gillrakers. The composition of the stock of fish is that of Lake Karats with the exception that pike constitutes 12 % of the fish caught at test fishing.

As in other lakes having a low percentage of whitefish with a high number of gillrakers, the *Triaenophorus* invasion is low (Table 9). The relatively high proportion of pike does not seem to influence the invasion of *T. crassus* to such an extent that it could dominate other decisive features.
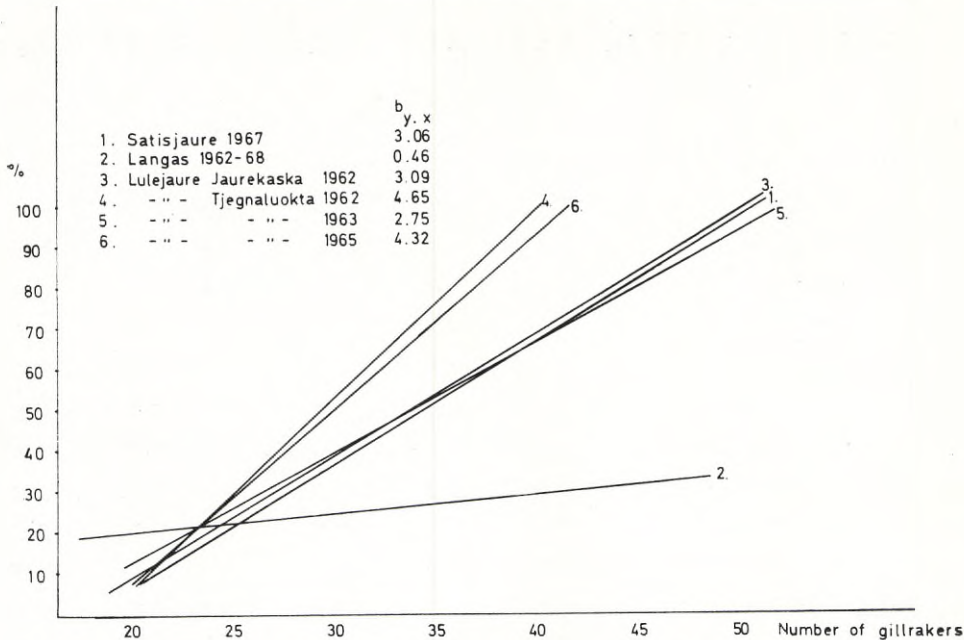
Fig. 19. Infestation by *Triaenophorus crassus* in whitefish in relation to number of gill-rakers in lakes in Stora Lule älv river system.

c. The Stora Lule älv river

Satisjaure (10)

The lake is 440 m above sea level and has an area of 47.7 km². In 1964 the lake was regulated with an amplitude of 11 metres. From 1966 the regulation was extended up to 457 m above sea level with a total amplitude of 19 metres.

The western part of the lake has the characteristics of a mountainlake; the shores are wooded and birch trees predominate. The eastern part (Patats), however, has flat shores and the trees are mostly pines.

The composition of the stock of fish was established by extensive test fishing, before there had been any changes due to the regulation. The following numbers give the percentage distribution:

	Trout	Char	Grayling	Whitefish	Pike	Perch	Burbot
East Satis (Patats)	0.5	6.0	15.8	62.9	1.2	2.0	11.7
West Satis	0.8	21.5	3.2	63.3	—	0.2	11.0

In the western part of the lake no pike has been caught in spite of many years of test fishing, and the occurrence of pike is low even in the eastern part; yet there is a high frequency of whitefish infested with *T. crassus* (Table 10). In the material examined, whitefish with a rather low number of gillrakers are more infested in Patats than in the western part of Lake Satis, but the difference is not significant.

Table 10. Infestation by *Triaenophorus crassus* in whitefish in lakes from Stora Lule älv river system.

Locality		\	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	Total
																	Number of gillrakers														
Satisjaure west 1966:	No. examined		—	—	—	—	—	—	—	—	—	—	—	—	—	33	—	—	—	—	—	—	—	—	—	—	—	—	—	—	33
	„ infested		—	—	—	—	—	—	—	—	—	—	—	—	—	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12
	% „															36.4															
Satisjaure west 1967:	No. examined		—	—	—	—	—	—	—	1	—	3	5	3	4	3	1	—	—	2	2	5	8	2	2	2	2	1	—	—	49
	„ infested		—	—	—	—	—	—	—	1	—	1	1	—	1	1	1	—	—	2	1	4	6	1	1	2	2	1	—	—	26
	% „																								80.0						53.1
Satisjaure east (Palats) 1967:	No. examined		—	—	—	—	5	3	3	13	15	7	10	4	31	7	12	10	7	12	15	—	2	4	21	6	7	—	—	2	215
	„ infested		—	—	—	—	1	1	1	2	4	—	4	2	21	1	8	8	4	9	10	—	2	2	6	6	4	—	—	1	116
	% „															62.3															54.0
	No. of worms /inf.							16.7																							
Langas 1962:	No. examined		—	—	—	—	2	—	4	16	9	16	18	13	6	1	7	2	2	3	—	2	1	—	—	—	—	—	—	—	111
	„ infested		—	—	—	—	1	—	1	7	2	7	6	5	—	1	4	1	2	2	—	2	—	—	—	—	—	—	—	—	40
	% „															35.9															36.0
Langas 1963:	No. examined		—	—	—	—	2	3	12	5	6	4	8	2	3	3	—	—	—	1	1	—	—	—	—	—	—	—	—	—	50
	„ infested		—	—	—	—	1	—	5	1	5	2	1	—	3	1	—	—	—	1	1	—	—	—	—	—	—	—	—	—	21
	% „																														42.0
Lulejaure Luspen 1960 XII	No. examined		—	—	—	—	2	3	2	2	5	3	2	3	1	2	1	2	—	—	—	—	1	—	—	—	—	—	—	—	30
	„ infested		—	—	—	—	1	1	1	—	3	1	2	2	1	2	1	2	—	—	—	—	1	—	—	—	—	—	—	—	16
	% „							44.0																							53.3
	No. of worms /inf.																														1.7
Tjegnaluokta 1962 X	No. examined		1	—	1	1	2	9	6	7	10	9	8	4	4	4	5	10	7	16	6	13	7	6	5	—	1	—	—	—	140
	„ infested		—	—	—	1	1	1	3	4	4	7	5	3	3	3	4	9	6	15	4	11	6	5	5	—	1	—	—	—	99
	% „							50.8													86.1										70.7
	No. of worms /inf.																														2.0
Jaurekaska 1962 X	No. examined		—	—	—	1	4	2	8	8	5	8	2	3	3	1	1	—	1	1	1	2	—	—	—	—	—	—	—	—	50
	„ infested		—	—	—	1	1	2	2	4	1	4	—	3	2	—	1	—	1	1	1	1	—	—	—	—	—	—	—	—	20
	% „							38.6													2.1										40.0
	No. of worms /inf.																														1.9
Älloluokta 1963 XII	No. examined		—	—	—	—	—	1	1	—	—	—	—	—	—	—	1	1	1	1	1	4	1	2	2	1	1	1	—	—	16
	„ infested		—	—	—	—	—	1	1	—	—	—	—	—	—	—	1	1	1	1	1	4	1	2	2	1	1	1	—	—	15
	% „							1.9																							93.7
Tjegnaluokta 1963 X	No. examined		—	—	—	2	6	10	15	24	29	23	35	24	13	7	5	4	5	4	6	5	9	6	—	—	—	—	—	—	232
	„ infested		—	—	—	1	3	4	4	6	10	8	11	8	7	3	4	3	3	4	2	5	7	4	—	—	—	—	—	—	90
	% „							32.0													62.7										38.7
	No. of worms /inf.																														1.6
Tjegnaluokta 1965 X	No. examined		—	—	—	2	—	1	5	4	4	4	6	9	4	4	5	3	13	11	7	12	8	10	5	2	1	—	—	—	120
	„ infested		—	—	—	1	—	1	1	3	3	1	4	4	3	3	4	3	11	11	6	11	8	8	5	2	1	—	—	—	92
	% „							48.7													90.1										76.6
	No. of worms /inf.							1.6													1.8										

Table 11. The feeding habits of whitefish in Lake Langas during January—December. Abbreviations see Table 4.

	F-%		D-%	
	23—31 gr	32—40 gr	23—31 gr	32—40 gr
Copepoda	6.5	31.6	6.5	26.3
Bosmina	—	5.3	—	5.3
Eurycercus	17.4	15.8	13.0	10.5
Chironomidae	56.5	42.1	39.1	26.3
Trichoptera	8.7	—	2.5	—
Hydracnidae	2.2	—	2.2	—
Lymnea	13.0	15.8	6.5	10.5
Valvata	21.7	15.8	10.9	10.5
Sphaeriidae	28.3	15.8	15.2	10.5
Empty	42.5	34.5	—	—
Number examined	85	24	—	—

As will be seen from Fig. 19, there is a marked increase in *Triaenophorus* infestation in the whitefish with an increased number of gillrakers. The regression coefficient is $b_{y,x} = 3.06$.

Langas (12)

The lake is 375 m above sea level and has an area of 55 km². It is a forest lake immediately downstream from the waterfall Stora Sjöfallet. At test fishing the fish caught had the following composition: char 3.9 %, trout 1.3 %, grayling 6.8 %, whitefish 81.1 %, pike 0.4 %, perch < 0.1 %, burbot 6.6 %.

There are no differences between the various parts of the lake according to the composition of the stock of whitefish. Different species cannot be separated.

The *Triaenophorus* infestation has been investigated from several localities in the middle of the lake (1963) and in the eastern part (1962). No significant difference between the two years was found (Table 10). One test from the western part of Lake Langas, taken in 1963, shows that 38.4 per cent of 45 specimens of whitefish examined were infested with *T. crassus*. Specification by number of gillrakers was not done.

As is shown by test fishing, the pike population is very small. The spawning places of the pike are mainly concentrated in a bay in the eastern part and three bays in the middle of the lake. As regards *Triaenophorus* infestation there seem to be no differences between whitefish from different parts of Lake Langas.

The whole population shows the same degree of infestation with *T. crassus*, which constitutes a difference from all the other lakes reported above. This indicates that the choice of food is probably uniform. The choice of food for 109 specimens of whitefish examined is reported in Table 11. The material comes from lesser tests, taken at various times but relating to 7 months (January—March, July—September, December). If for whitefish the number

of gillrakers is more or less than 32 differences can be stated. When compared with the conditions in other lakes, however, the frequency of *Copepoda* in whitefish with a low number of gillrakers is high.

The distribution of numbers of gillrakers shows no peaks which would indicate different species of whitefish. It is, indeed, level for gillraker numbers between 20 and 40, with a maximum at about 29. Consequently introgression has gone far. According to SVÄRDSON (1958) two closely related species must have different ecological niches to be able to live together. If their niches are identical, one species will soon drive out the other.

Thus, if introgression has been large-scale, one could expect a lesser difference of *Triaenophorus* invasion in whitefish with different numbers of gillrakers than in lakes where the different species are well separated, even if the groups compared present the same difference in number of gillrakers. The regression line for the *Triaenophorus* invasion, with regard to whitefish with different numbers of gillrakers, actually turns out to be very level (Fig. 19). There is no significant difference between whitefish with more than 32 gillrakers and those with fewer.

Lulejaure (13)

Lake Lulejaure is situated 369 m above sea level with an area of 165 km². The shores are flat and covered with coniferous forest.

The stock of fish according to test fishing is composed of: trout 3.2 %, grayling 9.5 %, whitefish 74.5 %, pike 4.7 %, perch 2.5 % and burbot 5.6 %.

Here, too, the introgression between different species of whitefish has proceeded far, but two maxima for numbers of gillrakers can be discerned, *viz.* about 30 and 37.

The samples from Tjegnaluokta (Table 10) were taken in October just before spawning time, when the whitefish assemble at areas with a depth of 15—24 metres. The test fishing should give samples from the same population, as it was made at the same time for different years within this concentrated area. This was obviously the case in 1962 and 1965.

Comparisons regarding the choice of food cannot be made, since whitefish caught near spawning time mostly have an empty stomach. In the few cases, where food was found, all specimens had eaten *Bosmina*.

The differences between the whitefish species as regards invasion by *T. crassus* (Fig. 19) are considerably greater than, for instance, in the lakes of the Lilla Lule älv river system (*cf.* Fig. 18). The value of P in a t-test was less than 0.001.

The influence of lake regulation upon the frequency of *T. crassus* and *C. truncatus* in whitefish has been published elsewhere (PETERSSON 1971). Hence no results from impounded lakes (localities 44—47, 51) are presented here.

d. The River Lilla Lule älv and the River Stora Lule älv (the proper river)
(15, 27)

With regard to the occurrence of the first intermediate host, *Copepoda*, there can be expected for flowing water a lower invasion of *T. crassus* in the second intermediate host.

Whitefish tests have been taken at the following localities, the distance from the river mouth in the Gulf of Bothnia being given in brackets: Kall- udden (150 km), Mattisudden (160 km) and Storsand (100 km). The popula- tions are stationary, with an average of 26—29 gillrakers.

Further down the river the populations are mainly composed of sea-migra- ting whitefish, and their parasite fauna is partly dependent on the conditions in the coastal area: thus, they do not represent the parasitiocoenosis of the river proper.

The rate of invasion is lower than in the lakes lying higher up for white- fish with corresponding numbers of gillrakers. At Mattisudden no infested whitefish was found, and at Kalludden and Storsand the infestation by *T. crassus* was 16.7 and 10.0 per cent respectively.

The food of the whitefish examined consisted entirely of bottom animals, particularly *Ephemeridae* and *Pallasea*.

e. Coast of the Gulf of Bothnia within the county of Norrbotten and the lower reaches of the Torne älv, Kalix älv and Lule älv rivers (43, 6, 5)

The coastal area of Norrbotten has two species of whitefish: C. nasus, which spawns near the coast and is stationary the whole time within the coastal area; C. *lavaretus*, which migrates up the rivers to spawn but for the rest resides in the coastal areas. Taggings (PETERSSON 1966) have shown that the whitefish spawning in the river after spawning time leave the river and from each river go further southwards. These migrations can extend very far: a distance of 150—300 km is not unusual. On hatching, most of the fry from C. *lavaretus* leave the river (LINDROTH 1957). C. *nasus* is sta- tionary within a restricted area.

The Triaenophorus invasion in the two species is reported in Table 12. Although the numbers of gillrakers overlap, the tests show a marked dif- ference between Junkön and other localities. The whitefish from Sandöfjärd fully corresponds to the river whitefish and is C. *lavaretus*; the Junkö white- fish is consequently C. *nasus*. The invasion of *T. crassus* is markedly higher in this latter species and is in accordance with the conditions in coastal ciscoes.

The result indicates that there may be greater differences in living circum- stances than was previously supposed.

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Table 12. Infestation by *Triaenophorus crassus* in *Coregonus nasus* and *C. lavaretus* from coastal areas.

Locality		Number of gillrakers																Total
		21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	
Lule archipelago Junkön (43) X.62	No. examined	1	2	7	6	11	9	7	3	—	3	1	—	—	—	—	—	50
	infested		—	2	3	1	5	2	1	—	—	—	—	—	—	—	—	14
	%																	28.0
Lule archipelago Junkön (43) VI.64	No. examined	2	1	5	7	6	10	8	3	3	—		—	—	—	—	—	46
	infested		—	1	3	1	2	3	2	—			—	—	—	—	—	12
	%																	26.1
Lule archipelago Sandöfj. VIII.62	No. examined			—	—	2	3	5	7	9	6	10	2	2	2	2	—	50
	infested			—	—	—	1	1	—	1	—	1	—	—	—	—	—	4
	%																	8.0
River Lule älv Vittjärv (30) VIII.62	No. examined			—	—	—	4	4	7	10	10	8	4	1	1	—	1	50
	infested			—	—	—	—	1	1	1	3	—	1	—	—	—	—	7
	%																	14.0
River Kalix älv Kamlunge (6) VIII.62	No. examined			—	—	—	1	10	6	10	8	9	4	1	2	—	—	51
	infested			—	—	—	—	1	—	2	—	1	—	1	—	—	—	6
	%																	11.7
River Torne älv Kukkola (5) VIII.62	No. examined			—	—	—	2	4	3	10	12	6	4	4	3	2	—	50
	infested			—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
	%																	0

Table 13. Infestation by *Triaenophorus crassus* in *Coregonus albula*.

Locality	No. exam-ined	Per cent infested by *T. crassus*
Sandträsket (7)	105	0.0
Kusträsket (33)	85	18.8
Kidträsket (36)	24	0.0
Ören (55) spring spawning (1965) ..	23	60.9
„ — (1966) ..	33	54.5
Ören (55) autumn spawning (1965) ..	30	10.0
„ — (1966) ..	24	20.8
Madkroken (57)	20	20.0
Flåren (58)	30	23.3
Sunderbyn (32)	15	13.3
Kalix archipelago		
Storöhamn (42)	117	28.2
Pålängefjärden (41)	80	27.5

f. Infestation by *T. crassus* in ciscoes (*C. albula*)

Ciscoes from the following six lakes were examined:

Sandträsket (7), county of Norrbotten, catchment area of River Råne älv; stock: pike, perch, roach, burbot, whitefish, cisco.

Kusträsket (33), county of Norrbotten, Lule river system, 1.1 km²; stock: pike, perch, burbot, whitefish, cisco.

Kidträsket (36), county of Västerbotten, Malån river system.

Ören (35), county of Jönköping, Motalaström river system, 196 m above sea level, 9.6 km²; stock: pike, perch, roach, char, whitefish, cisco.

Madkroken (57), county of Kronoberg, Mörrumsån river system, 195 m above sea level, 12 km²; stock: pike, perch, whitefish, cisco and eel.

Flåren (58), county of Kronoberg, Lagan river system, 151 m above sea level, 39 km²; regulated in 1923; stock: pike, perch, roach, bream, eel, whitefish and cisco.

There have further been examined tests from the archipelagoes of Lule and Kalix and a rather small test from the lowest reach of the Lule älv, Sunderbyn, 20 km from the mouth of the river.

The infestation of *T. crassus* are reported in Table 13. They are every-where of modest proportions, with the exception of spring-spawning ciscoes in Lake Ören. In all the lakes there is an amply supply of pikes.

According to MILLER (1952) ciscoes were considerably more infested with *T. crassus* than were whitefish, if they occurred in the same lake. In lakes with only whitefish, *Triaenophorus* could often not be found. The author considered ciscoes to be the natural intermediate host, as, in regard to growth, they were less affected by strong attacks of *T. crassus* than were whitefish. As will be seen from the comparison made in Table 14, these conditions are not valid here. In spite of the fact that in all four cases the whitefish involved have an average of less than 30 gillrakers, the invasion of plerocercoids is higher in whitefish than in ciscoes or is at least equally

Table 14. Infestation by *Triaenophorus crassus* in *Coregonus albula* compared with whitefish from same localities.

Locality	Per cent infested by *T. crassus*	
	Ciscoes	Whitefish
Ören (55)	57.1 spring spawn	81.8
„ —	14.8 autumn spawn	—
Madkroken (57)	20.0	26.7
River Lule älv		
Sunderbyn (32)	13.3	—
Heden-Vittjärv (31, 30)	—	14.3
Archipelago		
Storöhamn-Pålänge (42, 41)	27.9	—
Junkön (43)	—	26.1

high. According to SVÄRDSON (1957 a) ciscoes feed on pelagian planktons, and would thus be exposed to a high risk of infestation. The samples from the lowest reach of the Lule älv migrate from the coastal area up into the river to spawn, as do the whitefish with which a comparison is being made. The tests from the archipelago consists of ciscoes and whitefish, which both grow up and spawn within the same coastal area. Thus, all the samples will be comparable from an ecological point of view. A greater tendency for ciscoes to be infested with *T. crassus* cannot be deduced from the material presented. It should, however, be considered that the ciscoes from the coast of Norrbotten were younger than the whitefish with which a comparison was made. For Lakes Ören and Madkroken this difference did not occur.

In Lake Ören there are both spring and autumn spawning ciscoes. The test material has been caught both in spring and autumn, and it has been possible to separate the two types by reference to the development of the gonades. The autumn spawning type predominates in number. The difference in *T. crassus* invasion in the two types is statistically significant ($P < 0.001$).

For the present, no explanation can be given of the fact that there is a higher invasion in the spring spawning type than in the autumn spawning type.

According to SVÄRDSON (1957 b), it has been established that spring spawning cisco has a smaller scale central field, which would mean that the first growing season is effectively shorter. This would suggest that during the first year the spring spawning cisco would have even less possibility than the autumn spawning cisco of being invaded, since the hatching is produced so late in comparison with the spawning time of pike. Besides, the spring-spawning type goes very deep to spawn. The ciscoes examined were caught at the beginning of June at a depth of 25—30 m.

The two types show no difference as regards attacks from *Diphyllobothrium osmeri* (*cf.* Table 15), which has the same intermediate host as

Table 15. Infestation by *Diphyllobothrium osmeri* and *D. dendriticum* ( ) in whitefish.

Locality	Loc. No. (cf. Fig. 1)	Number examined	No. of gill-rakers	% infested specimens	No. of gill-rakers	% infested specimens	Total population	
							% infested	No. of cysts /infested fish
Kårtjejaure 1967 VII	11	74	26—38	100.0 (8.1)	—	—	100.0 (8.1)	27.4 (1.0)
Satisjaure 1966, 1967 IX	10	55	26—35	37.5 (2.5)	36—45	40.0 (6.7)	38.2 (3.6)	3.4 (1.0)
Kakerjaure 1967 IX	8	12	26—36	33.3 (8.3)	—	—	33.3 (8.3)	4.8 (1.0)
Vojmsjön 1961 VII—IX	45	98	17—26	41.2 (—)	36—52	9.9 (13)	15.3 (1.0)	2.5 (1.0)
Vaikijaure 1961 IX	22	103	20—29	14.9	30—37	13.3	14.6	—
„ 1966 VII		28	22—29	19.0	30—36	11.9	17.9	
Purkijaure 1961 IX	21	208	18—29	21.3	30—42	31.3	24.5	2.5
Randijaure 1961 VIII—IX	20	95	18—28	61.0	33—52	44.4	57.9	2.7
Parkijaure 1959 VI—VIII, X	19	167	18—33	39.4	35—53	45.2	41.9	3.2
Skalka 1961 VII, X	18	87	21—24	33.3	40—54	42.5	41.4	4.4
Langas 1963 I—XII	12	97	23—32	49.3	33—42	55.6	50.5	—
Lulejaure 1962 X (Tjegnal.)	13	93	20—32	59.6	33—42	63.0	61.3	—
„ 1962 X (Jaurek.)		50	23—32	75.3	33—39	83.3	76.0	—
„ 1965 X (Tjegnal.)		119	24—32	66.7	33—44	57.5	60.5	
Storuman 1961 VIII—IX	44	96	19—26	56.3	35—47	16.8	36.5	1.8
Malgomaj 1961 VIII—X	46	133	18—27	43.9	30—45	30.3	36.1	3.9
Flåsjön 1961 VIII—X	51	92	20—26	43.8	28—40	14.3	19.6	2.7
„ 1963 XI		23	19—27	26.1			26.1	3.5
Tåsjön 1961 VIII—X	47	—	—	—	25—46	5.0	5.0	—
„ 1962 VIII		—	—	—	38—45	0.0	0.0	—
„ 1963 XI		—	—	—	35—47	0.0	0.0	—
„ 1964 VIII		—	—	—	36—46	2.9	2.9	—

T. crassus with the exception that invasion can occur throughout the summer. Put together, these facts mean that a food segregation between the two types would only occur in early spring.

B. *Diphyllobothrium osmeri* and *D. dentriticum*

There are few investigations on the rate of invasion of these cestods in whitefish from Scandinavia and Finland. VIK (1957) occasionally examined specimens of whitefish in connection with investigations in lakes with char and trout. BYLUND (1966) reported on a larger body of material from Lake Enare in the north of Finland, as also did WIKGREN (1964) from Lake Joensuu in the east of Finland, the material in this case mostly consisting of ciscoes.

Most of the material was frozen before examination, so it was not possible to force out living larvae with pepsin solution, as can be done with newly captured fish. Larvae enclosed in cysts deep in the stomach musculature might have escaped discovery, especially in rather big specimens; for big whitefish, however, such a risk exists only when the stomach is rather empty, in which case the stomach wall was thick. The liver was cut in thin slices, so that it was possible to discover all larvae there. The numbers given for the invasion of *Diphyllobothrium* larvae should, however, be regarded as minimum values.

For a description of the localities from which the material has been taken, see above under the heading *Triaenophorus*; Lakes Kårtjejaure and Kakerjaure have not been mentioned before.

Kårtjejaure (11) is a deep fjeld tarn, 415 m above sea level with an area of 7.8 km². It has steep, rocky shores. Stock of fish according to test fishing: trout 0.1 %, char 33.9 %, whitefish 64.2 % and burbot 1.7 %.

Kakerjaure (8) is the easternmost lake in the Teusa valley, north of the Stora Lule älv river, 440 m above sea level and with an area of 4.0 km². It is relatively shallow, and surrounded by steep rock faces. Stock of fish according to test fishing: trout 1.8 %, char 19.6 %, grayling 15.0 %, whitefish 44.4 % and burbot 19.3 %. Since 1964 the lake has been part of the Satis water store and perch has thus appeared.

Invasion of *D. dendriticum* in whitefish was found only at four localities; in all cases only to a very small extent. On the other hand, invasion of *D. osmeri* was very common; in one case, Lake Kårtjejaure, it covered 100 per cent of the stock (Table 15).

A characteristic feature for all the lakes where whitefish was infested by *D. dendriticum,* is the simultaneous occurrence of char. Test fishing has shown that char constituted 33.9 per cent of the total catch in Lake Kårtjejaure, 8.0 per cent in Lake Satisjaure and 19.6 per cent in Lake Kakerjaure. In Lake Vojmsjön there were only solitary specimens of char in the catch. Only a small number of *D. dendriticum* pleocercoids were found, yet a

connection can be seen between infestation and the proportion of char in the stock of fish: lakes with a greater occurrence of char display an increased invasion of *D. dendriticum*. In all the cases the intensity of the infestation was low, with an average of only 1.0 plerocercoid per fish infested.

After attention was drawn to the fact that infestation of *D. dendriticum* in whitefish will only appear in lakes with char, tests were made on char from Lake Kårtjejaure in July 1967. There are two types of char in the lake: one is small and feeds mainly on bottom animals, the other is a somewhat bigger form and feeds on plankton. Of the first type 10 specimens were examined: 8 had no cysts of *Diphyllobotrium,* 2 carried each 2 cysts with *D. dendriticum.* Of the second type also, 10 specimens were examined: they were all infested by *D. dendriticum* (15 cysts per specimen) and 4 were in addition infested by *D. osmeri* (3.3 cysts per infested specimen).

The results here given correspond to the conditions in Lake Enare in the north of Finland, as found by BYLUND (1966). There, the invasion of *D. dendriticum* was in char 100 per cent, in whitefish 0 per cent, in dwarf whitefish 0.8 per cent; and that of *D. osmeri* in char was 62.5 per cent, in whitefish 61.6 per cent and in dwarf whitefish 11.5 per cent. The whitefish species were not specified.

The number of fish infested by *D. dendriticum* in the various lakes is too small to allow a study of the invasion in different species of whitefish.

D. dendriticum is to be regarded as a secondary parasite in whitefish, char being the primary host. The specificity of a parasite is seldom absolute. If there is a high invasion in a species of fish, and the species concerned is rich in individuals, even a host that is not normal for the parasite can be infested.

The invasion of *D. osmeri* in whitefish with different numbers of gillrakers gives a very heterogeneous picture (*cf.* Table 15). For 13 localities, where the distribution in numbers of gillrakers has admitted of a division of the material, the frequency of infestation was in 7 cases highest in whitefish with less than 30—32 gillrakers, while in 6 cases it was highest in whitefish with a greater number of gillrakers. A t-test, however, has only given significance for the difference in three cases (Table 16). At these localities *C. pidschian* and *C. nasus* were most infested.

As is the case with *Triaenophorus crassus,* the fish is invaded by Diphyllobothrid plerocercoids, because *Copepoda* with procercoids are part of the food. There is, however, a difference: the invasion of *T. crassus* is concentrated within a rather short period in spring, while infestation with *Diphyllobothrium* can occur throughout the whole growth cycle.

In non-regulated lakes there was a great difference in infestation with *T. crassus* in various species of whitefish: the highest frequency was found in whitefish with a high number of gillrakers; it appears that such a ten-

Table 16. Difference in infestation by *Diphyllobothrium osmeri* in whitefish with more and less than 30—32 gillrakers.

Locality	P	Infestation greatest in whitefish with > 30 gr respectively < 30 gr
Vaikijaure	0.9 > P > 0.8	< 30
Purkijaure	0.2 P 0.1	> 30
Randijaure	0.2 P 0.1	< 30
Parkijaure	0.5 P 0.4	> 32
Langas	0.7 P 0.6	> 32
Lulejaure 1962	0.8 P 0.7	> 32
„ 1965	0.4 P 0.3	< 32
Storuman	P < 0.001	< 30
Malgomaj	0.2 > P > 0.1	< 30
Vojmsjön	P < 0.01	< 30
Flåsjön	P < 0.001	< 30

dency is not valid for *D. osmeri*. This circumstance could, among other things, be due to the fact that the segregation in the choice of food is different for different periods. Nilsson (1960) found a tendency towards increased segregation in autumn. There is no material of such an extent as to show the real situation early in spring. The material on the choice of food reported above mostly relates to whitefish caught in autumn, thus implying a higher degree of differences in the choice of food than in summer. As has been previously demonstrated, the differences in the choice of food between different species of whitefish have turned out to correspond to equivalent differences in infestation with *T. crassus*. Since the invasion of *D. osmeri* extends throughout the growth cycle, the invasion in whitefish of different species can be expected to show less marked differences than if the invasion was concentrated within autumn or early spring.

It is well known that Diphyllobothrid larvae can pass from a prey fish to a predator (Kuhlow 1953 a, Dogiel 1964). Fish, although in small quantities, forms part of the food of whitefish, and according to results from Lake Vojmsjön, to a greater extent in *C. pidchian* than in *C. peled* (Nilsson

Table 17. Infestation by *Diphyllobothrium osmeri* in *Coregonus albula*.

Locality	No. examined	Per cent infested by *D. osmeri*
Sandträsk	10	20.0
Kusträsk	28	28.6
Sunderbyn	15	66.7
Storöhamn	15	46.7
Ören (autumn spawning)	44	9.1
„ (spring „	34	12.2

Table 18. Infestation by *Proteocephalus* spp. in whitefish.

Locality	Loc. No. (cf. Fig. 1)	Number examined	No. of gill-rakers	% infested Pyloric	% infested Intestine	No. of worms/infest. fish Pyloric	No. of worms/infest. fish Intestine	No. of gill-rakers	% infested Pyloric	% infested Intestine	No. of worms/infest. fish Pyloric	No. of worms/infest. fish Intestine	Total % infested (pyloric)
Vaikijaure 1961 IX	22	103	20—29	20.3	—	—	—	30—39	13.8	—	—	—	18.4
„ 1966 VII	—	21	22—29	47.6	—	3.1	—	—	—	—	—	—	—
Randijaure 1959 VII—X	20	293	18—29	25.8	—	—	—	30—52	34.0	—	2.9	—	28.7
„ 1961 IX	—	101	18—28	0.0	—	—	—	33—52	30.0	—	—	—	—
Parkijaure 1959 VI—X	19	162	18—32	35.1	—	4.3	—	35—53	42.4	—	5.8	—	38.3
„ 1961 IX	—	10	—	—	—	—	—	34—53	50.0	—	—	—	—
„ 1966 VIII	—	20	18—32	33.3	—	—	—	34—53	75.0	—	—	—	50.0
Skalka 1961 IX	18	81	—	—	—	—	—	40—53	24.7	14.8	3.8	—	—
Storuman 1961 VIII—IX	44	96	19—26	25.0	2.1	6.5	1.0	35—47	33.3	12.5	8.4	2.0	29.2
Malgomaj 1961 VIII—X	46	133	18—27	0.0	0.0	—	—	30—45	1.3	3.9	1.0	2.3	0.8
„ 1962 V, X	—	68	19—27	5.9	0.0	—	—	30—44	38.2	26.5	6.2	4.6	22.1
Vojmsjön 1961 VII, IX	45	98	18—27	23.5	—	4.8	—	36—52	51.9	13.6	11.9	7.2	46.9
Flåsjön 1961 VIII—X	51	92	20—26	9.4	7.7	—	—	28—34	3.7	13.6	—	—	4.3
„ 1963 XI	—	26	20—29	3.8	1.5	—	—	—	—	—	—	—	—
Tåsjön 1961 VIII—X	47	140	24—35	14.3	—	9.1	—	39—45	28.5	14.3	5.4	4.4	15.7
„ 1962 VIII	—	18	—	—	—	—	—	38—45	87.5	56.5	3.8	3.1	—
„ 1963 XI	—	47	—	—	—	—	—	35—47	27.7	31.9	—	9.1	—
„ 1964 VIII	—	34	—	—	—	—	—	36—46	67.7	61.8	5.0	3.3	—
Lulej. Tjegnal. 1962 X	13	68	23—22	10.8	13.5	5.3	8.4	33—42	22.6	35.5	2.9	—	16.1
Jaurek. 1962 X	—	50	23—32	18.2	27.3	4.6	7.2	—	—	—	—	—	—
„ Tjegnal. 1963 X	—	20	23—32	20.0	46.7	1.0	11.2	—	—	—	—	—	—
„ Alloluokta 1963 XII	—	16	—	—	—	—	—	34—46	31.3	62.5	5.6	3.2	—
„ Tjegnal. 1965 X	—	119	24—32	5.1	23.1	1.5	4.4	33—44	15.0	41.3	4.8	4.2	11.8
Langas 1963 I—XII	12	120	23—32	15.6	22.9	6.6	6.6	33—42	8.3	25.0	5.5	4.5	14.2

1958). A certain accumulation effect could therefore be possible for white-fish with a low number of gillrakers.

Within a parasitocoenos there can be a certain antagonistic relation be-tween different parasite species. There seems to be a negative correlation between the number of cysts of the nematode *Raphidascaris acus* and *D. osmeri*. *R. acus* being the most common in whitefish with a high number of gillrakers, even this circumstance counterbalances the rate of invasion in whitefish with a high and a low number of gillrakers.

A high consumption of *Copepoda* throughout the year and, in consequence, an expected high infestation by *D. osmeri* occurs to be neutralized by the above-stated three factors.

The infestation in cisco (Table 17) was low except in the case of two small tests from Sunderbyn (32) and Storöhamn (42). Both these tests consisted of ciscoes from the coastal area. The cisco caught at Sunderbyn goes up the river only to spawn.

It has not been possible to establish a difference in infestation frequency between ciscoes spawning in spring and in autumn, as was the case for *Triaenophorus crassus*.

C. *Proteocephalus* spp.

Since to a great extent it has not been possible to carry out determination of species (*cf.* p. 136), the material will be treated as a unit.

On examination of infestations by *Proteocephalus* spp. three types of evolution have been found: (a) adult tapeworms in the pyloric part of the intestine; (b) larvae about 2—4 mm, also in the pyloric part of the intestine; (c) larvae at the end of the intestine.

Owing to the seasonal variation in *Proteocephalus* (MOLNAR 1965, DOGIEL 1961, CONNOR 1953), different lakes have been compared only if the tests were taken at similar periods.

A comparison between different species of whitefish (Table 18) shows that in all cases, except Lake Vaikijaure in 1961 and Lake Flåsjön in 1961, the infestation was higher in whitefish with a high number of gillrakers than in species with a lower number of gillrakers. As for *Triaenophorus crassus*, the rate of invasion is correlated with the difference in the choice of food between the whitefish species. There is a high invasion among plankton eaters.

In order to measure the difference in infestation between the whitefish species in the various lakes, the invasion in whitefish with a low number of gillrakers has been calculated as a percentage of infestation in whitefish with a high number of gillrakers (Table 19). There is a great scattering, greater for *Proteocephalus* than for *T. crassus*. It is true that the average is higher for *Proteocephalus,* but the difference is not statistically significant.

Table 19. Infestation by *Proteocephalus* spp. and *Triaenophorus crassus* in whitefish with less than 30 gillrakers as percentage of infestation in whitefish with more gillrakers.

Locality	Per cent	
	Proteo-cephalus spp.	*Triaenopho-rus crassus*
Vaikijaure -61	147.1	25.6
Randijaure -59, -61	54.0	27.0
Parkijaure -59, -66	67.4	54.3
Storuman -61	75.8	98.1
Malgomaj -61	17.3	23.7
Vojmsjön -61	45.3	64.3
Tåsjön -61, -64	39.6	102.6
Langas -62, -63	188.0	100.5
Lulejaure -62, -65	47.4	54.8
Mean	75.8	61.6

In absolute numbers there is a lower rate of infestation with *Proteocephalus,* but it concerns a tapeworm with a life cycle of one year; concerning *Triaenophorus* there is an accumulation effect. Thus comparison can only be made for young fish.

The number of adult worms in infested specimens was often around 5 and seldom more than 10. A marked divergense from this was noted in two cases. In Lake Stora Lulejaure the number of adult worms and larvae was on average 3.5 (1—7) for each infested specimen, apart from one whitefish with 46 parasites. In the archipelago of Härnösand the number of adult worms averaged 6.4 (1—17) for each infested individual, but in one individual there were 97 parasites. In these two exceptional specimens of whitefish the stomach contents consisted of sticklebacks. Otherwise whitefish usually do not feed on fish. NILSSON (1962) has shown that fish can specialize in their choice of food; in these circumstances a consumption of fish may be usual.

Table 20. Infestation by *Proteocephalus* spp. in *Coregonus albula*.

Locality	Month	No. examined	Percentage infested by	
			Adults	Larvae
Kidträsket	X	12	8.3	—
Ören spring spawning	V	16	—	18.8
„	VI	33	—	—
Ören autumn spawning	VI	24	—	—
„ —	XI	20	—	—
Madkroken	IX	20	10.0	—
Sandträsket	IX	15	100.0	20.0
Sunderbyn	X	15	26.7	53.3

The foregoing would imply that *Proteocephalus* can be carried on from one fish to another. DOGIEL *et al.* (1961) supposes it to be a secondary character that *Proteocephalus* has no second intermediate host. Besides, there are two species not occurring in Sweden, *P. ambloptitis* in Amia and *P. pinguis,* which have fish as a second intermediate host.

The invasion in cisco corresponds to the conditions in whitefish (Table 20).

It is remarkable that neither adult individuals nor larvae were found in the pyloric in cisco from Lake Ören. The same is valid for the whitefish from the same lake, though larvae were found at the end of the intestine in 45 per cent of the material. The fish was caught during three months: May, June and November. Consequently there could possibly be a species which cannot settle down in whitefish nor in cisco. The procercoids cannot be determined in species.

VII. Infestation in relation to the age of the whitefish

A. The parasite fauna in one-year-old whitefish

Young whitefish was caught in the lakes of the Lilla Lule älv river system (17—22). A gill net of nylon with a mesh perimeter of 40 mm was used, and the fish thus caught measured 8—15 cm. This means that occasionally it was possible to catch one-summer-old whitefish during their first autumn. The greater proportion of the material obtained consisted of one-year-old whitefish (1+) 9—12 cm long; a small proportion were two years old (2+) and 14 cm long. Thus the net proved to be particularly selective as to length,

Table 21. *Triaenophorus crassus* infestation in one-year-old whitefish in lakes in River Lilla Lule älv and at Storsand, River Lule älv.

Locality	Number of gillrakers	Number examined	Number infested	Per cent infested
Randijaure (20) VII 1964	< 30	22	3	13.6
	> 30	61	15	24.6
„ — VIII 1966	< 30	18	2	11.1
	> 30	23	5	21.7
„ — VIII 1967	< 30	40	1	2.5
Parkijaure (19) VIII 1966	< 30	41	8	19.5
	> 30	9	6	66.7
Skalka (18) VIII 1964	< 30	47	4	8.5
„ — VI 1966	< 30	34	4	11.8
	> 30	1	1	—
„ — IX 1967	< 30	40	5	12.5
Tjåmotisjaure (17) VI, VII 1964 ...	< 30	64	11	17.1
Purkijaure (21) VIII 1967	< 30	40	3	7.5
Storsand				
Lule River (28) IX 1963	< 30	25	1	4.0

Table 22. The feeding habits of young whitefish in lakes in River Lilla Lule älv.

Locality	Number of gillrakers	Month	Copepoda		Cladocera excl. Euryc.		Eurycercus		Ostracoda		Chironomidae		Trichoptera		Ephemeridae		Asellus		Hydracnidae		Sphaeriidae		Terrest. insects		Empty
			F	D	F	D	F	D	F	D	F	D	F	D	F	D	F	D	F	D	F	D	F	D	F
Purkijaure	< 30	Aug.	7.1	—	28.6	14.3	78.6	57.1	—	—	28.6	7.1	—	—	—	—	42.9	21.4	—	—	—	—	—	—	6.7
Randijaure	< 30	Aug.	13.5	—	43.2	35.1	43.2	37.8	—	—	40.5	24.3	5.4	—	2.7	—	8.1	2.7	2.7	—	—	—	—	5.3	9.8
	> 30	Aug.	34.2	5.3	81.6	78.9	13.2	10.5	—	—	5.3	—	—	—	—	—	—	2.6	2.6	—	—	—	5.3	—	17.4
Parkijaure	> 30	Aug.	25.0	12.5	75.0	50.0	25.0	12.5	6.3	—	37.5	18.8	6.3	6.3	—	—	—	—	—	—	6.3	—	—	—	15.8
	> 30	Jun.	71.4	71.4	78.6	28.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	22.2
Skalka	< 30	Jun.	33.3	—	66.7	53.3	13.3	—	6.7	—	66.7	46.7	—	—	—	—	—	—	—	—	—	—	—	—	16.7
	< 30	Aug.	3.2	—	16.2	16.2	29.1	16.2	9.7	3.2	80.6	61.3	6.5	3.2	—	—	—	—	3.2	—	3.2	—	—	—	31.1
Tjåmotisjaure	< 30	Jun.-Aug.	—	—	36.4	30.3	9.6	6.0	3.0	3.0	66.7	51.5	15.2	9.1	—	—	—	—	3.0	—	3.0	—	—	—	13.2

and consequently age, and the results obtained reflect mainly the invasion in whitefish of the age of $1+$.

In 1964, with the exception of Lake Randijaure, only juveniles of *C. pidschian* were caught. In 1966 the net was occasionally allowed to float from the surface of the deeper parts of the lakes; a greater distribution in species was then obtained. In 1967 the net was again used as a bottom net and with occasional exceptions only *C. pidschian* was caught. These circumstances indicate an obvious selection in dwelling places for the different species of whitefish in their second year of life. In all, 425 specimens of one-year-old whitefish have been examined.

Triaenophorus crassus

The frequency of infestation by *T. crassus* in one-year-old whitefish is shown in Table 21. For whitefish with fewer than 30 gillrakers there were small differences between the various lakes. Further, the differences in infestation between the different species of whitefish were smaller in one-year-old fish. Thus, it seems that the factors determining the rate of parasite invasion were relatively uniform for the first year of life.

During their second summer there was a very great consumption of planktons by all species of whitefish (Table 22). While *Copepoda* were very rarely found in the food of adult *C. pidschian-nasus*, they had a high frequency in young whitefish. The difference in plankton consumption between whitefish with a high and with a low number of gillrakers is markedly less in juvenile than adult fish; this has consequently resulted in a smaller difference in the rate of parasitation.

LINDSTRÖM (1962) has examined the biology of young whitefish in Lakes Storavan and Uddjaur and also their choice of food during their first summer. *Bosmina* dominated the food. The choice of food was influenced by place and cycle of calendar day; for the rest it was not possible to show any difference in the food selection of different species. During the second summer an increased setting to bottom animals was noticed in the choice of food of *C. pidschian-nasus*. Fishing with gill nets showed, that during the second summer *C. oxyrhynchus*, *C. peled* were most numerous in the pelago. It will thus be of interest to know whether the risk of invasion regardless of the choice of food may be greater for *C. pidschian-nasus*, dwelling closer to the shore; this circumstance will be discussed in more detail in section 10.

In the very shallow lakes Purkijaure-Randijaure the infestation by *T. crassus* in *C. pidschian-nasus* of the age of two summers had already reached almost the same level as for adult whitefish (with the exception of Lake Randijaure in 1967). In the upper lakes Parkijaure-Tjåmotisjaure, the invasion went further. The consumption of *Copepoda* decreased markedly in the two first-mentioned lakes, while in the latter two lakes whitefish was forced even

Table 23. Infestation by *Triaenophorus crassus* in fry of *Coregonus lavaretus* in cages in Lake Kusträsk.

Date	No. examined	No. infested by *T. crassus*	Per cent infested	Length of the fry (mm)
6.6	31	—	—	—
12.6	62	—	—	17—18
21.7	32	2	6.3	23—30
4.8	59	11	18.6	26—45

when adult to feed more on planktons at certain periods (*cf.* Figs. 8—11), perhaps owing to the limited littoral.

It has proved to be very difficult to catch young whitefish during their first summer; to ensure a determination of the rate of parasitation for this period, fry from a hatchery were put into cages in Lake Kusträsk (33) immediately after hatching. The cages were in the form of cubes with the dimensions 1 m×1 m×1 m; they were furnished with nylon nets with a mesh of 1 mm. The cages were lowered to the bottom of the lake at a depth of about 0.7—0.8 m and at a distance of 10—15 m from the shore. Zooplankton organism could pass through the net. On May 26, 1964, about 1000 fry of *C. lavaretus,* taken from the Kusträsk hatchery, were put in each of the three cages.

Samples were taken in the months of June, July and August (Table 23). The ciscoes in the lake were infested in 18.8 per cent. For the whitefish in the cages the infestation may partly be due to the environment created by the test arrangements; *e.g.* growth was less than can be considered normal. Lindström (1962) reported the following average lengths for *C. pidschian-lavaretus-peled* in Lakes Storavan and Uddjaure: June 16, 15.0 mm; July 23, 46.1 mm; August 11, 88.3 mm. The small increase in length for the whitefish in the cages may have postponed the period when larger food objects than *Copepoda* and *Cladocera* could have formed part of the food. No other bottom-living organisms than *Chironomidae* seem to have been able to colonize the cages.

The consumption of *Chironomidae* increased gradually (Table 24). The

Table 24. Food items in *Coregonus lavaretus* during the first summer in cages in Lake Kusträsk.

	12 june		21 july		4 august	
	F-%	D-%	F-%	D-%	F-%	D-%
Copepoda	38.7	32.3	84.4	71.8	67.8	10.2
Cladocera	100.0	67.7	37.6	18.8	91.5	49.1
Chironomidae	9.7	—	18.8	9.4	45.8	40.7

same appears from the results of LINDSTRÖM (*l.c.*). A deviating factor is the high consumption of *Copepoda* in July. In Lake Storavan, *Bosmina* definitely predominated in the choice of food during this time. The cages, however, can hardly have been selective as to permeability of *Copepoda* and *Bosmina*, and so it is natural to suppose that this difference would occur even in natural conditions. For the rest, the choice of food is in full correspondence with the results of LINDSTRÖM (*l.c.*).

Examination was also made of a small number of young whitefish of *C. peled,* caught July 23, 1958, in free water in Lake Storavan during their first summer. Out of 19 specimens examined, one (5.3 per cent) was infested with *T. crassus.* The rate of invasion corresponds very closely to that in the cage tests of Lake Kusträsk from the same date. *Bosmina* predominated in the stomach contents: *Chironomidae* were occasionally found in four specimens.

In a sample of young whitefish, aged one summer, from Lake Tåsjön (47), caught in September 1963, 11.1 per cent were infested with *T. crassus.* The average number of gillrakers was 41.3. In young whitefish, aged two summers, the rate of invasion at the same date was 45.5 per cent.

Diphyllobothrium osmeri

As is the case with *T. crassus,* infestation with *D. osmeri* seems to be greater during the first two summers (Table 25) than during the further life of whitefish (*cf.* Table 15). Further comparisons cannot be made, as the infestation in different species of adult whitefish was very incoherent.

During the tests with cages in Lake Kusträsk, Diphyllobothrid larvae were found for the first time on June 12: a procercoid in the stomach. On July 21 two specimens, *i.e.* 6.3 per cent, were infested, while no cysts could be

Table 25. Infestation by *Diphyllobothrium osmeri* in one-year-old whitefish in lakes in River Lilla Lule älv.

Locality	No. ex-amined	18—29 gr		30—48 gr	
		Infested %	No. of cysts/inf.	Infested %	No. of cysts/inf.
Purkijaure VIII 1967	30	6.7	1.0	—	—
Randijaure VIII 1964	62	36.4	1.5	52.5	2.4
„ VIII 1966	38	26.3	1.1	50.0	1.7
„ VIII 1967	27	22.2	1.0	—	—
Parkijaure VIII 1966	30	0	—	33.3	2.3
Skalka VIII 1964	47	2.1	(3.0)	—	—
„ VI 1966	34	11.8	1.0	—	—
„ IX 1967	24	16.7	2.0	—	—
Tjåmotisjaure VI, VIII 1964	38	2.6	(3.0)	—	—

Table 26. Infestation by *Proteocephalus* spp. in one-year-old whitefish in lakes in River Lilla Lule älv.

Locality	No. examined	18—29 gr		30—48 gr	
		Infested %	No. of worms/ inf.	Infested %	No. of worms/ inf.
Purkijaure VIII 1967	30	—	—	—	—
Randijaure VIII 1964	62	9.1	2.0	15.0	1.3
„ VIII 1966	38	—	—	—	—
„ VIII 1967	27	3.7	—	—	—
Parkijaure VIII 1966	30	—	—	—	—
Skalka VIII 1964	47	8.5	2.0	—	—
„ VI 1966	37	—	—	—	—
„ IX 1967	24	20.8	2.3	—	—
Tjåmotisjaure VI, VIII 1964	38	13.2	1.8	—	—

found at the last testing on August 4; thus the number of young whitefish infested is very low. Of the ciscoes in the lake 28.6 per cent were infested.

In the material from Lake Storavan, taken on July 23 and consisting of young whitefish aged one summer, no Diphyllobothrid larvae were discovered.

Proteocephalus spp.

Only specimens from the pyloric part of the intestine were included in the investigation, as larvae in the other parts of the intestine were found only occasionally.

In all, 105 specimens from the material of 1966 were examined: they were all free from infestation. During other years the infestation varied greatly (Table 26).

The test with cages in Lake Kusträsk gave a negative result on June 6. On June 12, 62 specimens were examined and 1 larva was found, located in the intestine. The pyloric appendices had not yet been developed in the whitefish, then 17—18 mm long. Consequently it will not be possible for *Proteocephalus* to parasitize young whitefish at this stage of growth. On July 21 there were found, in 32 specimens examined, 2 young whitefish with *Proteocephalus* in the pyloric part of the intestine and 2 young whitefish with larvae in the rear part. In the last test, on August 4, 59 specimens were examined and only one larva was found; it was located in the pyloric part of the intestine.

Young whitefish from Lake Storavan, caught during their first summer at the end of July, showed no infestation with *Proteocephalus*.

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Table 27. Correlation of age of whitefish with frequency of *Diphyllobothrium osmeri*. ( )=number examined, gr=number of gillrakers.

Age in years	Purkijaure (21)		Randijaure (20)		Storuman (44)		Lulejaure (13) 1962, 1965		Flåsjön (51)	
	≤29 gr	≥30 gr	≤30 gr	≥31 gr	≤26 gr	≥35 gr	≤32 gr	≥32 gr	≤26 gr	≥28 gr
1	—	—	—	—	—	—	—	—	—	—
2	77 (26)	89 (9)	100 (5)	—	—	—	40 (5)	150 (4)	40 (5)	0 (3)
3	62 (29)	130 (13)	165 (23)	0 (2)	0 (1)	24 (17)	0 (2)	0 (1)	22 (9)	0 (4)
4	38 (37)	55 (20)	207 (14)	100 (4)	189 (9)	28 (18)	250 (4)	100 (4)	60 (10)	143 (14)
5	33 (27)	53 (13)	153 (15)	200 (4)	61 (13)	22 (9)	435 (15)	140 (25)	0 (1)	183 (6)
6	22 (9)	100 (4)	37 (8)	433 (3)	177 (13)	0 (3)	72 (7)	205 (19)	—	0 (2)
7	0 (3)	100 (1)	67 (3)	0 (2)	220 (5)	0 (1)	489 (18)	179 (43)	—	200 (1)
8	0 (1)	—	—	0 (1)	366 (3)	—	941 (23)	571 (24)	—	300 (1)
9	0 (1)	—	500 (1)	—	50 (2)	—	591 (31)	365 (17)	—	0 (1)
10	—	—	100 (1)	—	—	—	958 (7)	640 (5)	—	—
11	—	0 (1)	—	—	—	—	200 (2)	200 (1)	—	—

B. Adult whitefish

In lakes with a low rate of invasion, *T. crassus* showed no increase as fish grew older. If the rate of invasion was high, invasion increased with age up to about 7 years (PETERSSON 1971).

The state of things was about the same for the invasion of *Diphyllobothrium osmeri* (Table 27). Relatively speaking, Lake Lulejaure had a high rater of invasion. There the number of cysts per 100 specimens of whitefish increased even for whitefish aged up to 10 years.

Proteocephalus spp. (Table 28) increased up to the ages of 8—10 years in

Table 28. Correlation of age of whitefish with frequency of *Proteocephalus* spp. ( )=number examined, gr=number of gillrakers.

Age in years	Lulejaure (13) 1962, 1965		Vaikijaure (22) 1961		Storuman (44) 1961		Tåsjön (47) 1961—1964	
	≤ 32 gr	≥ 32 gr	≤ 29 gr	≥ 30 gr	≤ 26 gr	≥ 35 gr	≤ 35 gr	≥ 36 gr
1	—	—	—	—	—	—	—	—
2	0 (5)	50 (4)	9 (11)	0 (5)	—	—	50 (2)	200 (14)
3	50 (2)	0 (1)	45 (20)	17 (6)	0 (1)	53 (17)	68 (19)	214 (36)
4	0 (4)	150 (4)	0 (9)	0 (7)	144 (9)	383 (18)	48 (31)	159 (22)
5	7 (15)	28 (25)	50 (13)	86 (7)	177 (13)	410 (9)	170 (17)	810 (9)
6	0 (7)	11 (19)	0 (12)	0 (1)	69 (13)	765 (3)	0 (7)	125 (4)
7	73 (18)	54 (43)	0 (2)	0 (2)	0 (5)	200 (1)	450 (2)	100 (3)
8	74 (23)	129 (24)	0 (1)	—	0 (3)	—	—	300 (1)
9	42 (31)	130 (17)	0 (2)	—	1250 (2)	—	0 (1)	—
10	0 (7)	220 (5)	0 (1)	—	—	—	—	—
11	800 (2)	0 (1)	—	—	—	—	—	—

Table 29. Infestation by *Triaenophorus crassus*. Samples from several years.

Locality	No. of gill-rakers	Per cent infested										
		1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970
Vaikijaure (22)	20—29	—	11.5	—	—	—	—	11.6	—	—	—	—
	30—40	—	45.0	—	—	—	—	—	—	—	—	—
Purkijaure (21)	18—29	—	8.4	—	—	—	—	—	10.6	—	—	—
	30—47	—	17.5	—	—	—	—	—	16.1	—	—	—
Randijaure (20)	18—29	—	13.6	—	—	—	—	16.0	—	—	—	32.7
	33—52	—	50.0	—	—	—	—	58.3	—	—	—	—
Satisjaure (10)	21—47	50.9	45.2	—	—	—	50.0	—	53.1	—	—	—
Langas (12)	23—40	—	—	36.0	42.0	—	—	—	—	—	—	—
Lulejaure (13)	20—32	—	—	50.8	—	—	48.7	—	—	59.6	51.6	54.8
	33—42	—	—	86.1	—	—	90.1	—	—	90.7	94.7	83.8
Lule archipelago (43)	21—31	—	—	28.0	—	26.1	—	—	—	—	—	—
Tåsjön (47)	35—47	—	61.1	76.7	58.2	48.7	—	—	—	—	—	—

Lake Lulejaure, while in the other lakes invasion was at its highest in white-fish aged 5—6 years; for older whitefish the rate of invasion was lower. This is quite natural for a parasite with a cycle of one year, having regard to the decrease of consumption of planktons as fish grow bigger.

VIII. Long-term variation in infestation

The material now examined covers at most a period of 9 years. It appears that the frequency of invasion of *Triaenophorus crassus* was very stable (Table 29). Lake Satisjaure (10) was investigated during 8 years. There the rate of invasion was about 50 per cent from 1960 up to and including 1967. The specimens of whitefish examined in 1960 and 1967 belong to quite different age groups. Lake Lulejaure was investigated during five years from 1962 to 1970. There were only small differences in frequency of *T. crassus* between the years.

A comparatively large difference in the frequency of invasion was found only in Lake Randijaure (20) and in Lake Tåsjön (47). In the latter the

Table 30. Infestation by *Diphyllobothrium osmeri*. Samples from several years.

Locality	No. of gillrakers	Per cent infested					
		1961	1962	1963	1964	1965	1966
Vaikijaure (22)	19—37	14.6	—	—	—	—	17.9
Lulejaure (13)	20—44	—	61.3	—	—	60.5	—
Flåsjön (51)	20—27	43.8	—	26.9	—	—	—
Tåsjön (47)	35—47	0.0	0.0	0.0	2.9	—	—

Table 31. Infestation by *Proteocephalus* spp. Samples from several years.

Locality	No. of gillrakers	Per cent infested								
		1959	1960	1961	1962	1963	1964	1965	1966	1967
Vaikijaure (22)	20—29	—	—	20.3	—	—	—	—	47.6	—
Randijaure (20)	18—29	25.8	—	0.0	—	—	—	—	—	—
	30—52	34.0	—	30.0	—	—	—	—	—	—
Parkijaure (19)	18—33	35.1	—	—	—	—	—	—	33.3	—
	34—52	42.4	—	50.0	—	—	—	—	75.0	—
Flåsjön (51)	20—27	—	—	9.4	—	3.8	—	—	—	—
Tåsjön (47)	35—47	—	—	28.5	87.5	27.5	67.5	—	—	—

invasions in whitefish caught in 1963 and 1964 were significantly lower than that from 1962 (p < 0.05).

The annual rate of invasion is more immediately reflected by the conditions among young whitefish. Lakes Randijaure and Skalka offer samples from different years (*cf.* Table 21). It is true that there is a conformity between certain years; nevertheless, there are for other years variations which are greater than among adult whitefish.

Nor are there any marked differences between samples from different years as to invasion of *Diphyllobothrium osmeri*, (Table 30). In three out of four lakes there is a very great correspondence for different years; only in Lake Flåsjön is there a difference, which, however, is not significant.

Another picture is presented by *Proteocephalus* spp. The difference in invasion between different years is great (Table 31). It is natural to find a greater fluctuation of invasion in different years for a parasite with a one-year cycle of life, such as *Proteocephalus* spp. In *Triaenophorus* and *Diphyllobothrium*, where accumulation is made from year to year, differences of invasion between different years may be counterbalanced.

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Locomotory activity patterns of fourhorn sculpin, *Myoxocephalus quadricornis* (L.) (*Pisces*)

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I. Introduction

During the last decades a wealth of data has accumulated on biological rhythms. This applies to mammals, birds, fishes and invertebrates. The annual locomotory activity of fish from subarctic inland waters has been investigated for several years, but this type of investigation from marine and mixohaline environment is sparse. Investigations which deal with a limited part of the year are more abundant. Earlier, organisms were divided into night- or day-active ones in regard to the temporal patterns of their activity. In several species of fish, birds and mammals, it is imposible to point out only one of the phases mentioned. Among fishes this was first observed and described by Wikgren (1953, 1955), who investigated lampreys, *Petromyzon fluviatilis* L. and burbot, *Lota lota* L. Wikgren concluded that it was quite possible that the daily activity pattern is subject to changes during a year.

The present investigation deals with the fourhorn sculpin *Myoxocephalus quadricornis* (L.), a member of the family *Cottidae*. The fourhorn sculpin has a circumpolar distribution and occurs in both inland waters and in mixohaline environment.

The objects of this investigation were to find out the diel and seasonal periodicity, the annual level of activity, the activity during the spawning time as well as after the spawning, and finally to find out if a phase shift takes place in the Baltic population of fourhorn sculpin collected from its southern border of distribution. It has been shown recently, in another member of the family Cottidae, *viz. Cottus poecilopus* Heckel, that this species in South Sweden is night-active all year around (Andreasson, 1969) while in North Sweden a phase shift takes place in autumn and spring, and the fish is day-active in winter (Andreasson and Müller, 1969, Müller 1970 a).

II. Material and methods

This investigation was performed at the Askö Laboratory (58°50′N, 17°38′ E) south of Stockholm during the period December 1969 to April 1971.

Adult fourhorn sculpin were collected in the vicinity of the laboratory. After capture the fish were immediately placed under experimental conditions, a male alone in one aquarium and a female in an other. The aquaria were supplied with water from their natural habitat, the water intake being situated at a depth of 10 metres, which prevented diel fluctuations of the temperature. The bottoms of the two aquaria were covered with sand. The importance of low temperature to this species was pointed out earlier (WESTIN 1968). For this reason the temperature was not allowed to exceed 14°C. during the summer, the highest temperature in which fourhorn sculpin occur under natural conditions (McALLISTER 1959, WESTIN 1970 b). The temperature was kept below 14°C. by means of a refrigerator, Colora TK 64.

The activity of the sculpins was studied under natural light conditions (nLD). Various methods for measuring the activity of fishes have been described (SPENCER 1939, HEMPEL et al. 1956, MOORE 1961, LILLELUND 1967, MÜLLER and SCHREIBER 1967, DE GROOT 1968). In this investigation the method employed by MÜLLER and SCHREIBER (op. cit.) was used: a circular, double-walled aquarium, equipped with a window for a photocell to the light beam. The photocells, lamps, relays and transformers were supplied by Dr. BRUNO LANGE, Berlin. The lamps were shielded with infra-red filters. This method records the fish only at one particular point. The photocell was connected to a printer counter (Elmeg) which recorded the number of registrations per hour. The diel variation in activity was calculated as percentage deviation of 2 hour values from the corresponding 24 hour mean.

The spawning in this species takes place around the turn of the year. During the period 1970—71, the female was placed into the male's aquarium, since the male defends a territory of his own (WESTIN 1969, 1970 a). After spawning the female was immediately returned to her original aquarium.

The sculpins were fed at irregular intervals, mainly with fish, but sometimes with gammarids.

The fish used in the experiments were exchanged three times owing to accidents (female: May 15, June 24, male: March 7).

The terminology employed is according to ASCHOFF (1965).

III. Results

The annual level of activity

a. The female

In Fig. 1 the number of passages per 24 hours expressed as monthly average is shown with regard to the female. There are two peaks per year. The highest peak occurs in April, whereas the other, which is not so pronounced, is spred over three months (August, September and October). The lowest values were found in February and March 1970—71.
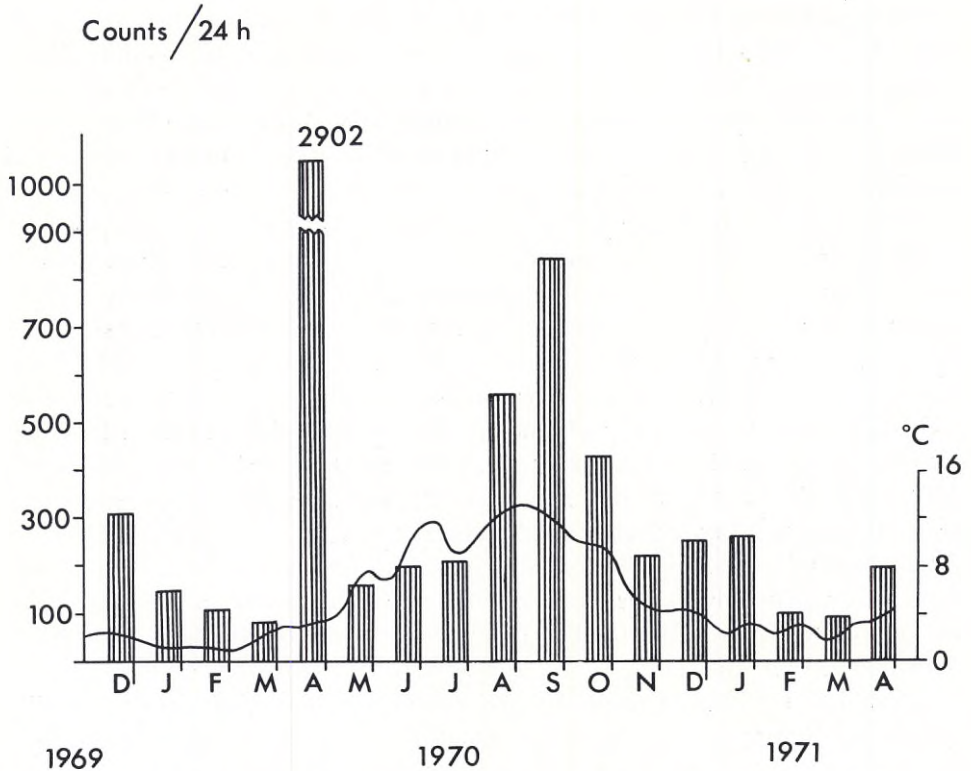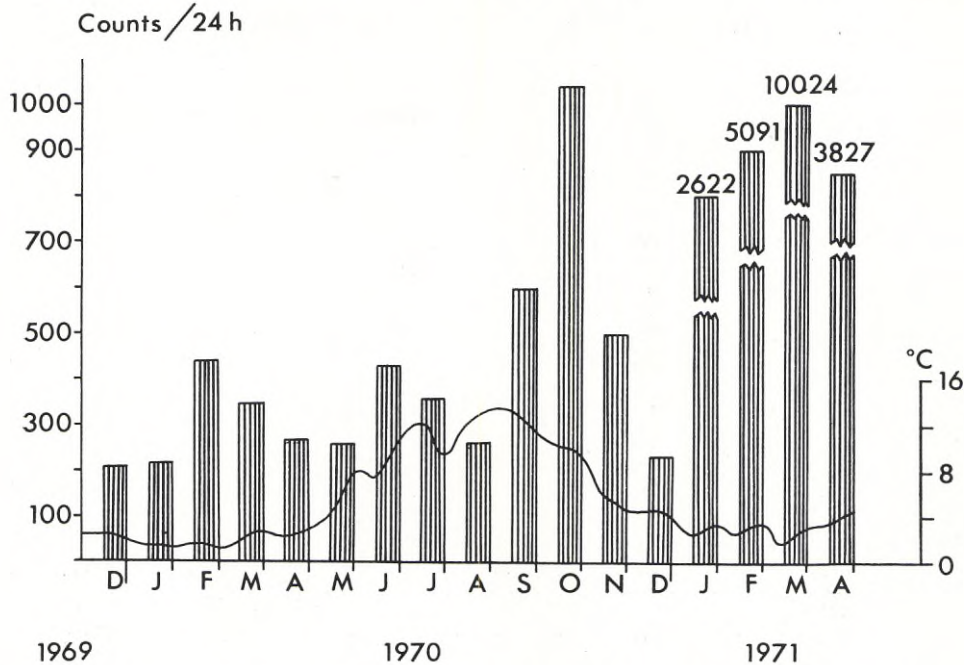
Fig. 1. Annual level of activity of a female fourhorn sculpin under natural light conditions. Left ordinate: number of registrations/24 hour as monthly average. Right ordinate: water temperature. Temperature indicated as a line. Values are lacking for the last decade in April 1971.

b. The male

In Fig. 2 the activity level of the male is presented in the same way as in Fig. 1. Except for the very high values in January—April 1971, the level of activity has only one peak, mainly around October. From December 1969 to September 1970 there are only minute differences between the months.

c. Spawning

As previously described the female was placed into the aquarium of the male on December 30, 1970. The spawning took place on January 2, which was also the date when the female was removed at midnight.

The average 24 hour values for the 10 days before spawning was 233 registrations for the female and 470 for the male. During the three days when the male and female were together the level of activity was 565, 1140 and

Fig. 2. Annual level of activity of a male fourhorn sculpin under natural light conditions. Left ordinate: number of registrations/24 hour as monthly average. Right ordinate water temperature. Temperature indicated as a line. Values are lacking for the last decade in April 1971.

2554 registrations, the mean value being 1419. The fertilization took place at dawn on the last of the three days mentioned.

d. Postspawning

In this species the male develops a parental behaviour and guards the egg mass until hatching while the female disappears from the nest after spawning (WESTIN, 1969). The level of activity of the female 10 days after spawning was lower than 10 days before, only 189 registrations.

The male differed strongly from the pattern described above. The number of activity registrations was very high immediately after spawning, and increased steadily during the period of egg guarding. In Fig. 3 the 24 hour mean of the decades from January to April are shown and the highest value is found during the last decade in March when the eggs hatched.

Diel and seasonal activity pattern of fourhorn sculpin

In Fig. 4 the diel activity pattern from December 1969 to April 1971 is shown. From the figure it is evident that the fourhorn sculpin twice a year
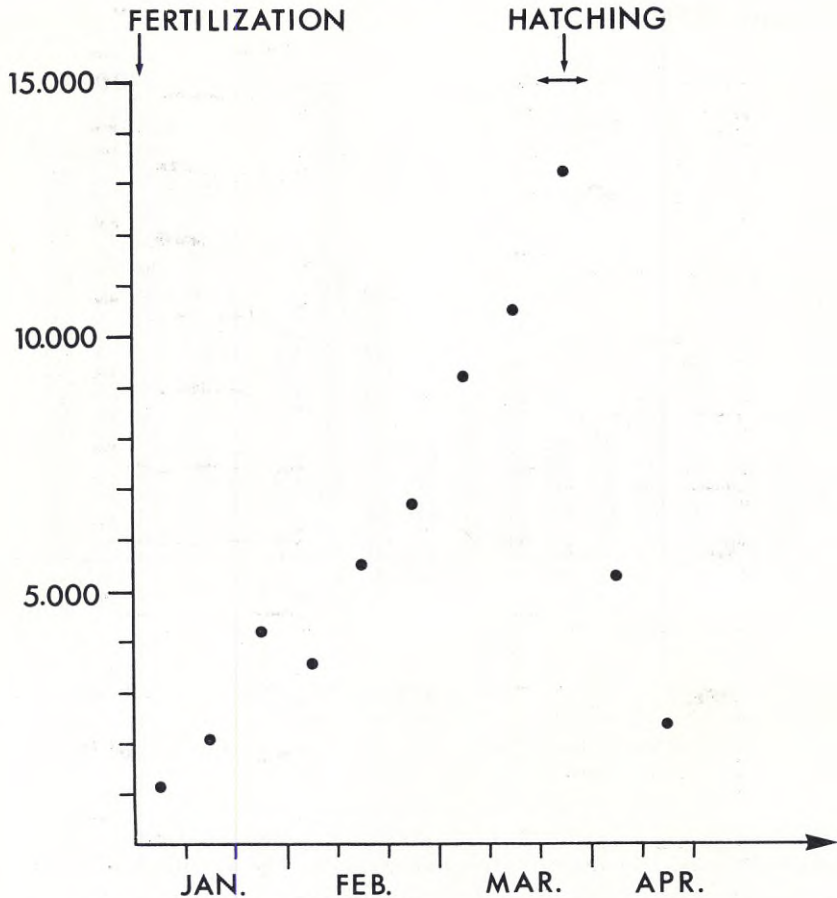
Fig. 3. Level of activity of a male fourhorn sculpin during the period of parental behaviour. Each point is the 24 hour mean of every decade. Ordinate: number of registrations.

changes its diel activity pattern from daytime during November—April to nocturnal activity during the rest of the year. Some differences exist, however, between the two fishes investigated. The female changed phase earlier than the male did, and during the first two months of the investigation some disturbance occurred as far as the female was concerned. Her activity was mainly concentrated to the evening in contrast to the male and to the conditions during the same time the next year. After these two months she shifted back to a daily activity pattern. Fig. 5 shows the temporal course of a phase shift during autumn.

First, there was a period of desynchronization but at the end of September the peak activity again occurred in the daytime. This period is followed by a second period of desynchronization characterized by a breaking down of
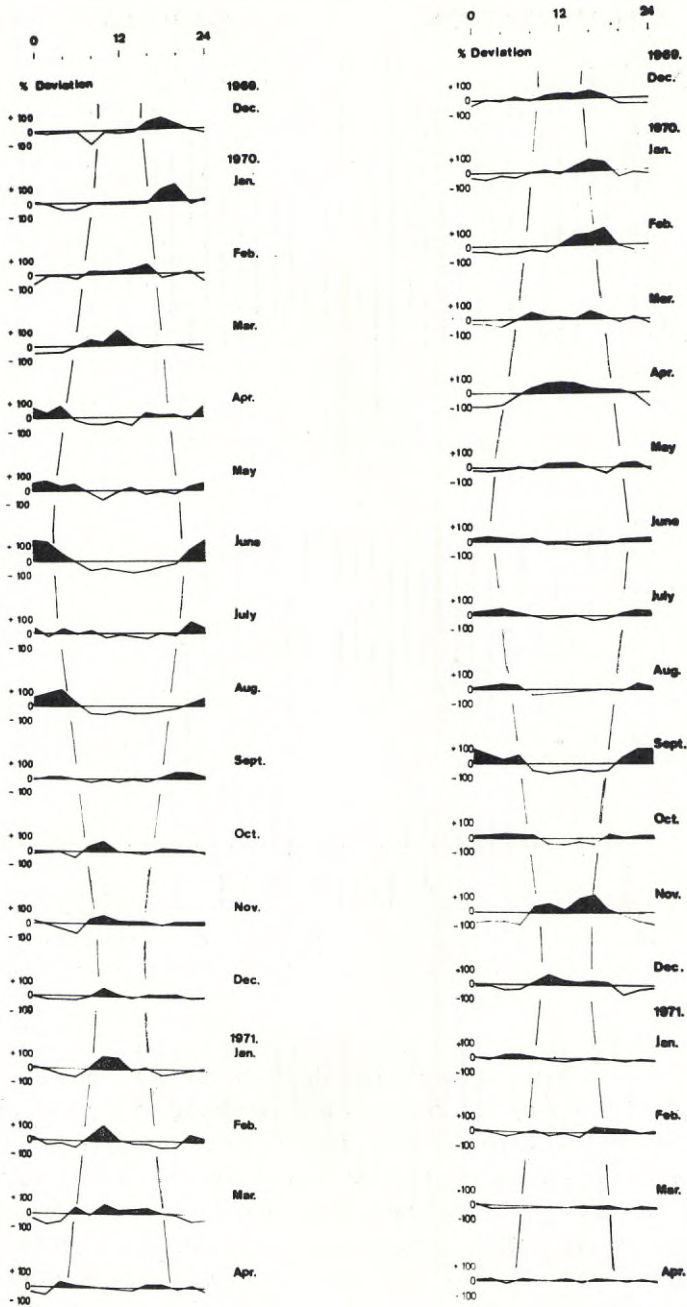
Fig. 4. Diel activity pattern of fourhorn sculpin under natural light conditions during a year, given as percentage deviation from the 24 hour mean. Vertical lines indicate sunrise and sunset. The female to the left, male to the right. Values are lacking for the last decade in April 1971.
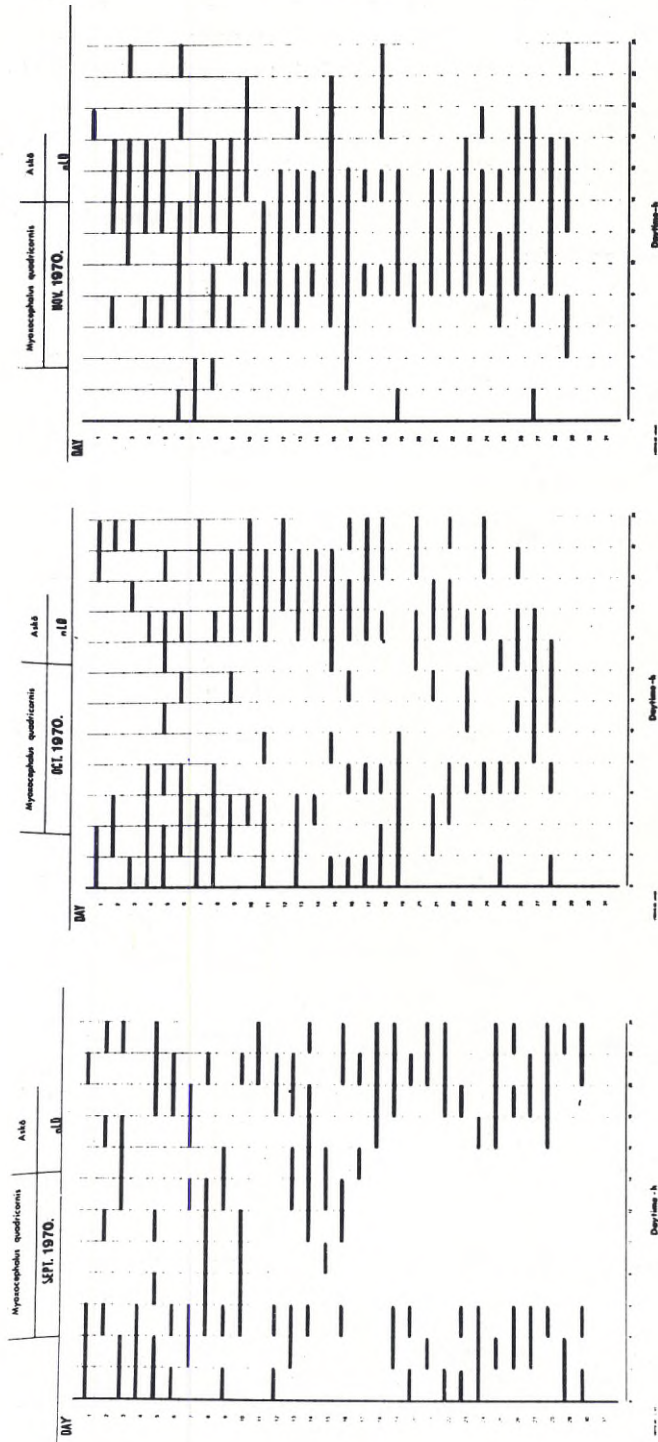
Fig. 5. The phase shift of the male of fourhorn sculpin in the autumn. The diel variation in activity is calculated as percentage deviation of 2 hour values from the corresponding 24 hours mean.

the confinement to the light—dark cycle, which acts as a Zeitgeber, and periods of activity occurred throughout each 24 hour period. Later on (November) the fish was again synchronized but now in the opposite phase.

During the second turn of the year, when the fourhorn sculpin had opportunity to spawn, some divergences were found also in the diel patterns in comparison with the first year.

The male was immediately before spawning synchronized to activity mainly during the day, while the female during the same period was desynchronized. When both fish were together in the male's aquarium, the general pattern may be characterized as desynchronized. It is impossible, however, to know if this is valid for both sexes because the number of registrations is the sum of the swimming activity performed by both sculpins. After spawning the female returned to a daily mode of life, while the male remained desynchronized during the entire period of parental care, which lasted for three months, and the difference in activity between day and night was very small.

IV. Discussion

The annual level of activity

The locomotory level of activity of the fourhorn sculpin varies during the year, Figs. 1, 2. The number of passages per 24 hour period expressed as monthly averages reflects to a certain extent the annual cycle of such physical factors as light intensity, length of day and temperature.

There was a pronounced variation of 24 hours means even within short periods, which does not only seem to be correlated to changes of the factors mentioned. It is recently shown (ERKINARO 1969, MÜLLER 1970 b), that, in connection with the phase shift the level of activity often increases. In the case of the female, the two peaks seem to coincide with the time prior to and during a phase shift. The same is true as far as the male is concerned with the exception that the peak expected in spring is practically absent. It is described, however, that the phase shift in spring is often of very short duration while in autumn it requires a longer period of time (ERKINARO 1969). The very high level of activity in January—April 1971 has no correspondence during the same period in 1970. Thus these very high values are due entirely to parental behaviour and will be discussed further below.

As the annual cycles of the three physical factors considered in this investigation coincide, it can not be stated from the activity values in nLD which exogene factor is the most important in controlling the annual level of activity when the high values owing to phase shift, spawning and parental behaviour are excluded. A close relationship between level of activity and

temperature is reported in *Cottus gobio* and *Cottus poecilopus* (ANDREASSON 1969, ANDREASSON and MÜLLER 1969). This does not seem to be the case where the fourhorn sculpin is concerned.

The activity level in connection with spawning

From the visual observations on the spawning of fourhorn sculpin in an aquarium it was noted that the level of activity rose when the light intensity decreased (WESTIN, 1969). This was true with regard to the behaviour in a crowded aquarium where only 2 males had opportunity to establish a territory of their own, and where weak light was allowed during the night to enable observations. During normal light conditions (nLD) and with only one male present in a well defined territory, the level of activity was rather low at that time. The same state of things applies to the female as well. When put together the spawning was of a short duration with a rising level of activity which was concentrated to dawn and dusk, the fertilization taking place at dawn. After spawning the female left the eggs and took no further part in the parental behaviour, and her level of activity decreased to a value lower than that before spawning.

The male, on the other hand, remained with the egg-mass until hatching, which began in the last decade of March when mean values of 24 hour periods was 13,214 registrations. It should be mentioned that the level of activity attained during the period of parental behaviour is not quite comparable to the level of activity during the rest of the year, because the male does not leave the eggs and thus is not swimming around in the aquarium the way he does during the 9 remaining months. The activity attained during the time of parental care consists of a turning around movement on the same spot, combined with a fanning activity with his fins. It is obvious, however, that the males care of the eggs originates at a high level of activity which steadily further increases and culminates at the end of the embryonic development, in connection with the hatching of the eggs. Also, the male defended the remainder of the egg-mass, which had developed fungus in the first decade of April, but during this time the level of activity had decreased. (Fig. 3.)

The diel activity pattern in connection with spawning

In December 1970 some slight differences in diel activity was noticed between the two sexes. Both had the activity located mainly in the daytime. At the end of this month, the normal spawning time, the male's activity was still linked to the daytime while that of the female was less synchronized. Also, from direct observations in connection with spawning, it is known that there exists a difference in behaviour because the male has dug a hole in

the soft bottom where he is waiting for a female who is swimming around restless some days before spawning (WESTIN 1969, 1970 a).

During the three days when male and female were put together, the combined pattern of their diel activity points to a desynchronization, with the highest number of registrations at dawn and dusk. After spawning the female returned to a daily mode of life. From investigations of the spawning in *Cottus gobio* it was noted, that the synchronization to light was distinct throughout the year and was broken only at the time of spawning. After spawning the synchronization to light was less pronounced than before (ANDREASSON 1969). Also in this species a parental behaviour occurs, this was, however, not investigated. In the burbot, a species which does not perform any parental behaviour, spawning took place in the daytime in spite of the fact that the fish had its activity phase during the night. In this species no desynchronization occurred (MÜLLER and ÖSTERDAHL 1970).

The phase shift

Twice a year the fourhorn sculpin changed its period of activity 180° in accordance with the Zeitgeber. The course of events started with the fish losing their regular shift between activity and rest and becoming desynchronized (Fig. 5). This state of things was reported i.a. also from *Salmo trutta* and *Cottus poecilopus* (MÜLLER 1969, 1970 a). After a period of desynchronization, the fish changes into a new phase. It is assumed that the phase shift is an adaptation to high latitudes because *Cottus poecilopus* from southern Sweden (55°35′N) had no phase shift (ANDREASSON 1969) whereas the same species from northern Sweden (66°42′N) changed phase (MÜLLER 1970 a). Previously it was uncertain whether the length of the day or the light intensity caused the shift of phase. Recently it has been shown, that the light intensity is the factor responsible for the shift (MÜLLER 1970 a, 1970 c), and in decreasing light intensity also *C. poecilopus* from southern Sweden changed from night-active to day-active in autumn (ANDREASSON and MÜLLER 1969, MÜLLER 1970 c). However, fourhorn sculpin close to its southern limit of distribution (58°50′N) changed phase twice a year. Thus the phase shift of the locomotory activity is a seasonal changing of the diel rytm of 180° in accordance with the Zeitgeber and as Zeitgeber acts the light—dark cycle.

In a recent investigation (WESTIN 1970 b) it was pointed out that fourhorn sculpin leave deeper areas and migrate to shallow areas. At the same time there is a change in the food habits of the species. A connection between phase shift and change of biotope is suggested in *Microtus* species (ERKINARO 1969). Is the phase shift due to the change of habitat or does it occur before the migration? No answer can be given regarding the temporal sequence but the light intensity is shown to give rise to the phase shift (op. cit.). If the fish migrates to shallow areas

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before the phase shift, the increasing light intensity would perhaps prevent the phase shift. On the other hand, if the phase shift comes first, it is known that once the phase shift is performed, higher light intensities do not influence the new pattern of diel activity (MÜLLER 1970 c).

From studies in *Petromyzon fluviatilis* it was stated that the pattern of activity most probably undergoes a radical change (from night to day activity) when the spawning starts (WIKGREN 1953), and also, studies on burbot have shown that the migration implies a connection with the spawning (MÜLLER 1970 b), and this state of things seems to be valid also for the fourhorn sculpin. Thus it may be assumed that the phase shift in the autumn is connected to the hormonal transformation before the spawning.

It was previously assumed that the migration to shallow areas in the autumn is due to the annual variation of the temperature, which is linked with a change in interspecific competition (WESTIN 1970 b). To the exogenous factors mentioned above the light intensity may also be added. The phase shift in the spring seems to occur when fourhorn sculpin still are to be found in shallow waters, since the phase shift took place in April—May and the sculpins remain in these areas until the beginning of June.

V. Summary

1. The diel and seasonal patterns and the annual level of locomotory activity in the Baltic population of fourhorn sculpin, *Myoxocephalus quadricornis* (L.) were investigated under natural light—dark conditions (nLD), and the diel activity was found to be synchronized to the light—dark cycle.

2. A phase shift occurs in the spring and the autumn and the fish is night-active during the summer and day-active in the winter. The phase shift was of short duration in the spring but extended over a longer period of time in the autumn.

3. The level of activity increased in connection with the phase shift.

4. Before spawning the activity of the female was less synchronized than that of the male, who was day-active.

5. During the spawning the combined pattern of the two sexes indicate a desynchronization and spawning took place at dawn. The combined levels of activity were higher than before spawning.

6. After spawning the female was synchronized to the natural light—dark cycle whereas the male was desynchronized during the time of parental behaviour which lasted for three months.

7. The level of activity of the male during the time of parental behaviour increased to very high values and culminated when the eggs hatched.

8. The migration which occurred in connection with the phase shift, when also the food fauna was changing, is discussed.

VI. Acknowledgments

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Bottom fauna and cooling water discharges in a basin of Lake Mälaren

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Contents

I. The area investigated

Morphometrics

The subject of this study, the Västerås Bay, is situated in the western part of Lake Mälaren. It comprises an area of about 50 km² including the adjacent bays of Fullerö and Ridö. The basin is to a large extent affected by outlets from the city of Västerås, which has about 100,000 inhabitants and is the most important harbour on Lake Mälaren.

The area studied can be divided into three sections with respect to the morphology of the basin and the localization of the sampling stations (Fig. 1). *Section I* covers the inner part of the Västerås Bay and is partly delimited from the outer areas by the islands Ö. Holmen, Elba and V. Holmen and the shallow bottoms between these. This part of the Västerås Bay receives the effluents of Västerås and the surrounding urban areas and can be expected to show the most striking effect of human influence. *Section II*

is made up of the outer parts of the Västerås Bay to Almö-Lindö. *Section III* which includes the bays of Fullerö and Ridö can be characterized as a transition area to the outer parts of Lake Mälaren.

Physico-chemical conditions

An important factor concerning the temperature conditions of the area is the localization of two fossil fuel power stations at the inner part of Västerås Bay (Fig. 1).

The total input of energy from the stations has been calculated for the period 17.XII.69—24.III.70 (EHLIN 1970). It amounted to $13.6 \cdot 10^{14}$ calories. About 25 % of the energy supplied remained in the basins inside Ridön, while 55 % was transported to outer parts of Lake Mälaren. The rest was given off into the atmosphere.

Generally taken the stations show a somewhat different picture as to the amount of energy supplied to the water body at peak operation. The outlet from Västerås power station has a large volume and a low overtemperature and emits a small part of the energy content to the atmosphere, while the outlet from Aroskraft power station through its higher over-temperature increases the temperature in the neighbouring area more conspiciously but contributes less to a temperature increase in the whole basin. The energy supply for the period mentioned above was for Västerås power station $9.4 \cdot 10^{14}$ calories, 17 % of which was given off into the atmosphere, and for Aroskraft power station $4.2 \cdot 10^{14}$ calories 29 % of which escaped into the atmosphere.

An excess of temperature caused by the discharges of cooling water is notable in the whole area. Thus, during the winter of 1969 outlets from Västerås power station increased the temperature of the bottom water in the bays of Västerås, Fullerö and Ridö. The rise was a little more than $0.5°C$ in the sounds at Ridön compared with the previous year. In July 1969 the temperature in Västerås Bay was about two degrees higher than in the outer parts of Lake Mälaren (*SMHI* 1969).[1]

The rather small depth of the area (10—12 metres — maximum 19 metres) prevents a stable stratification of the water layers, but, during periods of calm weather a metalimnion can be found at a depth of about 5 metres. The stratification is probably broken up by winds of 7—9 m/s (SMHI *op.cit.*).

The average oxygen content of the bottom water was 75 % during March and July in the period 1965—1969 (AHL, pers. comm.). Values around 50 % were recorded in July 1969 for many localities in the area (SMHI *op.cit.*). The surface water is constantly oversaturated during midsummer as a result of algal bloom.

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[1] SMHI stands for the Swedish State's Meteorological and Hydrological Institute.
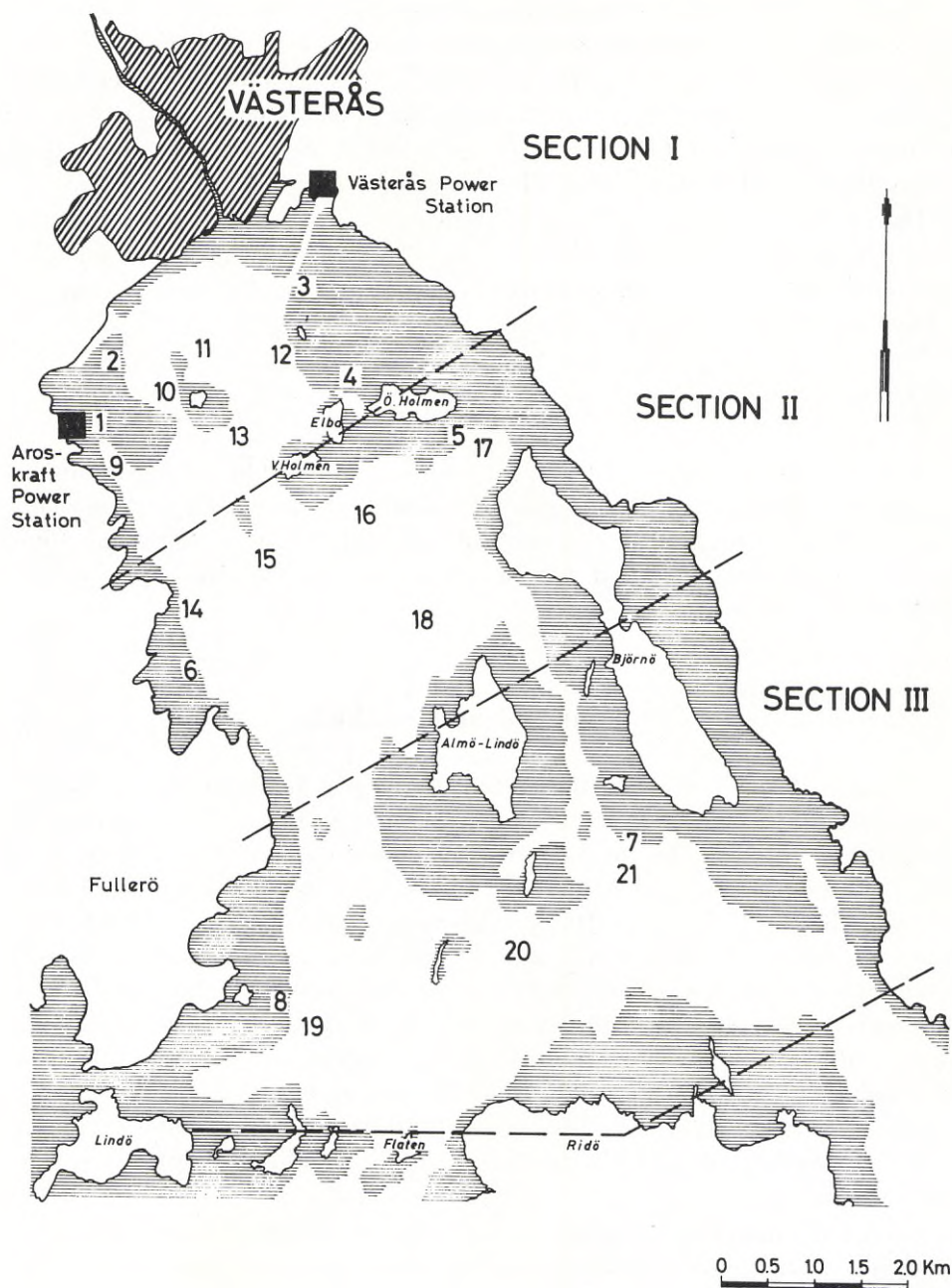
Fig. 1. Map showing the sites of the sampling stations. Shaded area — depth less than 6 meters.

The temperature increase has apparently not affected the oxygen situation in a negative way, which might have been expected because of the increased rate of decomposition of organic material. Instead the critical winter period is shortened by earlier ice-melting than during previous years (EHLIN *op.cit.*). Perhaps a reservation should be made for water layers quite near the bottom where the oxygen content can not be estimated with standard methods.

The content of plant nutrients of the surface water of Västerås Bay has been calculated for the period 1965—1969. The following values are averages of 18 measurements: total-phosphorus — 0.105 ± 0.024 mg/l, total-nitrogen — 1.253 ± 0.232 mg/l (AHL pers. comm.).

Phytoplankton

The phytoplankton exhibit a peak during the middle of the summer. Among the dominating groups can be mentioned species of *Melosira* and *Cryptomonas*. The greatest amount of phytoplankton is found at some distance from the town and not in the immediate vicinity of the outlets (SÖDERQVIST 1970).

II. Material and methods

The principal collecting of the bottom fauna was made in July 1969 with a sampler of the Ekman type at depths of 4 and 10 metres. The stations are presented in Fig. 1. The fauna of the shallow area near the effluent from Aroskraft power station was also sampled in February, March and October 1970. On each station 5 or 10 samples were taken, except in March 1970 when an apparatus of the KAJAK type was used and 20 random samples were taken within a square of 10,000 m² off Aroskraft. The bottom material was sieved through a net with the mesh size 0.6 mm and the sieve rest was preserved in alcohol. In the laboratory the material was sorted under a binocular of 6 times magnification and the wet weight determined with an accuracy of ± 0.1 mg. Altogether the material includes 240 samples with the EKMAN sampler and 20 with the KAJAK tube, containing a total of 15,106 individuals.

Besides the quantitative bottom material the chironomid fauna of the area has been studied more carefully through collection of imagines in 1970. The chironomids were netted at various points on the shore line in June, July and September. A few individuals were also collected from boat during the sampling of the bottom fauna in June 1969. After examination most of the species were checked against Professor L. BRUNDIN's large collection at the Museum of Natural History in Stockholm.
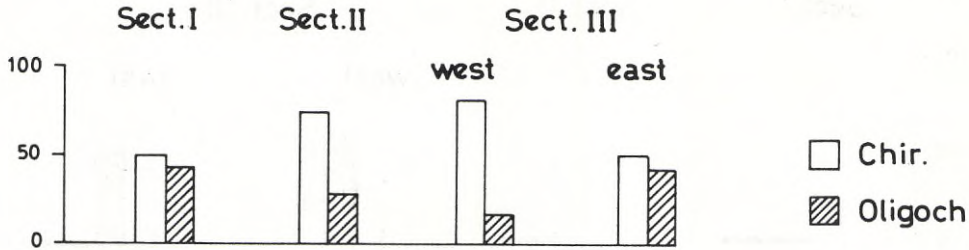
Fig. 2. Abundance of chironomids and oligochaetes as percentage of the total fauna. Depth: 10 metres.

III. Results and discussion

General part

A. *Large-scale survey of the fauna*

The bottom fauna of the area is dominated by chironomid larvae while oligochaetes are next in numbers. Very few pisiids and big crustaceans have been found. Among other members of the fauna are *Chaoborus* larvae and hydracarids. The composition of the benthos stresses the eutrophic character of the area.

The regional pattern of the fauna shows some striking trends that illustrate a pollution gradient from the inner part of the Västerås Bay towards the main parts of Lake Mälaren (Tab. 1 and 2, Fig. 2 and 3).

It may be seen from Fig. 2 that the oligochaetes constitute almost 45 % of the organisms on deeper bottoms in section I. In section II and the western part of section III their percental share of the fauna gradually diminishes, at the same time as the chironomids become more important. The divergent composition of the benthic community in the eastern part of section III reflects the complicated hydrological situation of this area affected by amongst other factors, an inflow of water through the sounds west of Ridön (SMHI *op.cit.*).

The chironomid fauna is characterized by the dominance of the groups *Tanypodinae* (almost entirely *Procladius spp.*) and *Chironomini. Tanytarsini* is sparsely represented and only a single *orthocladiin* (*Prodiamesa sp.*) has been found.

A remarkable fact is the frequent occurrence of *Chironomus* larvae of the *salinarius*-type on deeper bottoms of the area. The presence of this larval type, known as a brackish water form (THIENEMANN 1954, STRENZKE 1960), will be commented on elsewhere. Among other forms can be mentioned *Leptochironomus tener* KIEFF. and species of *Polypedilum* and *Cryptochiro-*
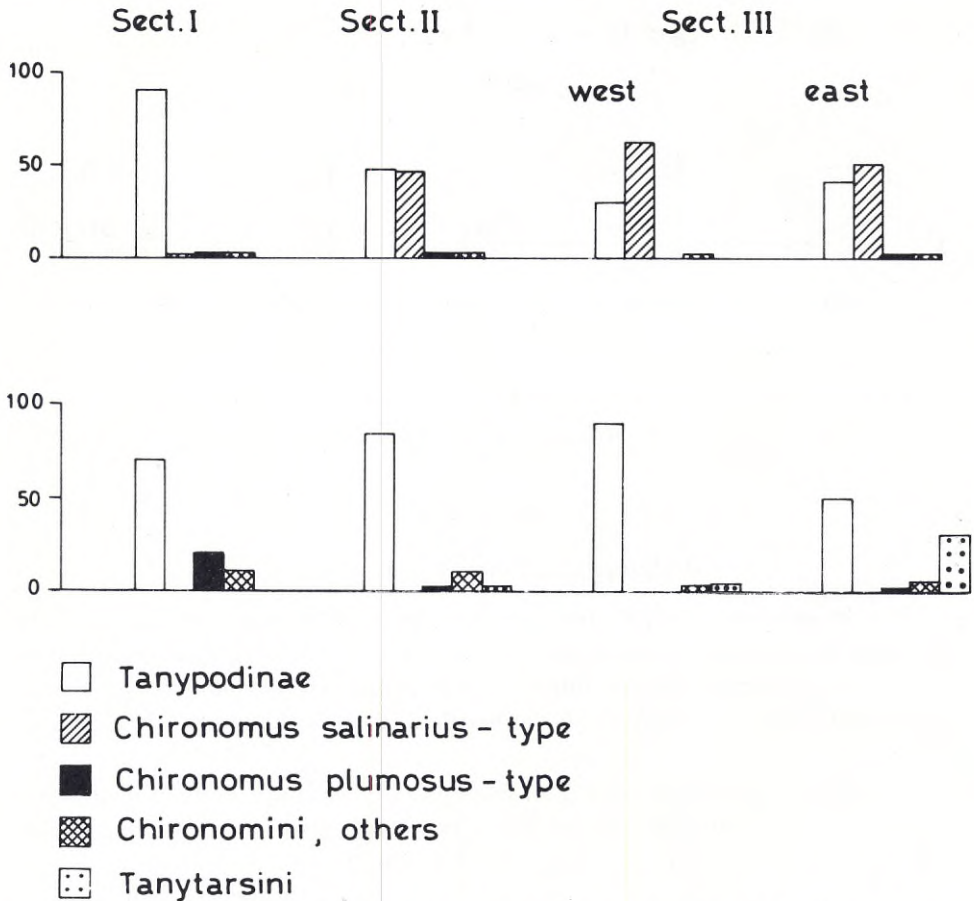
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Fig. 3. Composition of the chironomid fauna. In percentage of total larval abundance.
Above — 10 metres depth, below — 4 metres depth.

nomus on the deeper bottoms, together with a few *Paralauterborniella nigro-halteralis* MALL. and *Einfeldia sp.* in the shallow areas.

The regional variation of the chironomid fauna is at greater depth charac-terized by a complete dominance of tanypodins in section I (Fig. 3). In the outer part of the Västerås Bay larvae of the *Chironomus salinarius*-type be-come an important part of the fauna and in section III they constitute the dominating group.

On the shallower bottoms there is a tendency toward an increase of filtering organisms such as *Chironomus plumosus* in the inner part of Väster-ås Bay (Fig. 3). This is probably an effect of the more intense sedimentation of organic material on the large shallow bottoms in section I than in the more exposed bottoms of the outer areas. The occurrence of tanytarsins is typical of sections II and III and gives the fauna a littoral character.

Table 1 and 2 give some information on the variation within the different sections. Some of the values should be further commented on:

It appears that stations 11 and 12 hold a special position within section I. The oligochaetes are here especially abundant and account for 54 and 49 % of the fauna respectively. This makes them the dominating animal group and this is probably a result of adverse conditions caused by the proximity to the mouth of River Svartån and the harbour of Västerås.

The records of big crustaceans at stations 10 and 12 refer to single individuals of *Mysis relicta* LOVÉN. Scattered findings of *Pontoporeia affinis* LINDSTR. and *Pallasea quadrispinosa* SARS are typical of the shallow bottoms within sections II and III.

A remarkably large biomass is recorded at station 3. This is due to the abundance of both oligochaetes and chironomids. The area is probably to some extent a zone of sedimentation for organic material transported by the River Svartån. The large standing crop may be due also to the warm water effluents from Västerås power station. In fact a tendency to larger biomass is noted also for station 1, situated near the outlet of Aroskraft power station.

B. *The fauna near the warm water discharge*

Of special interest considering the effect of warm water discharges on benthic communities is the situation immediately off the outlets. It has already been pointed out that large biomasses were recorded near the power stations in July 1969.

The shallow area off Aroskraft has been studied more extensively and table 3 gives some of the results from samples taken within a distance of 500 metres from the effluent at different seasons.

When sampling it became evident that the nature of the bottom sediments is very heterogenous within the area. The bottom at station 101 and 104 (February 1970) was made up of hard clay with a very thin sediment layer of loose material, while the others had a thick layer of gyttja. Station 101 was situated quite near the outlet tube and station 104 between the points of intake and outlet. The diverging configuration of the sediment of these stations is probably a result of turbulence in the water, and is reflected very strongly in the composition of the bottom fauna. Thus the biomasses are much smaller than at stations 102 and 103, and the fauna is dominated completely by oligochaetes. In the further discussion stations 101 and 104 are not considered.

According to Table 3 the composition of the bottom fauna in 1970 was different from that of July 1969. While chironomids dominated in July 1969, oligochaetes formed the bulk in February 1970 and were further more important in March and October 1970.

Table 1. 10 metres depth. Abundance of the different animal

Section	I										
Station	9		10		11		12		13		Average
	ind/m²	%	ind/m²	%	ind/m²	%	ind/m²	%	ind/m²	%	ind/m² %
Chironomidae (larvae+pupae)	1520	58	1340	55	1250	43	1100	43	1220	61	1290 51
Oligochaeta	990	38	930	38	1580	54	1250	49	700	35	1090 43
Chaoborus	110	4	160	7	90	3	170	7	60	3	120 5
Hydracarina	20	<1	<10	<1	—	—	10	<1	<10	<1	<10 <1
Pisidium	—	—	—	—	—	—	—	—	—	—	— —
Big crustaceans	—	—	<10	<1	—	—	20	<1	—	—	<10 <1
Total fauna	2640±550		2430±330		2920±990		2550±740		1990±250		2510 —
Biomass g/m²	5.6± 2.2		7.3± 2.2		7.0± 2.7		6.7± 2.3		4.4± 2.1		6.2 —
Chironomid larvae:											
Tanypodinae	1230	84	1210	95	1110	92	990	92	1020	88	1110 90
Chironomus salinarius-type	60	4	20	1	—	—	<10	<1	40	3	30 2
C. plumosus-type	30	2	50	4	70	6	60	6	30	3	50 4
Chironomini, others	40	10	<10	<1	30	2	20	2	70	6	50 4
Tanytarsini	—	—	—	—	—	—	—	—	—	—	— —

This increased proportion of the oligochaete part of the fauna is most interesting, and a comparison with results from another part of Lake Mälaren with about the same trophic conditions is made in Fig. 4. The control area is situated in Svinnegarn Bay, a rather shallow bay outside the town of Enköping.

It appears that the balance between the main groups was about the same in both places in July 1969. *Chironomidae* was then the dominating animal group with 70—80 % of the total number of organisms, while *Oligochaeta*

Table 2. 4 metres depth. Abundance of the different animal

Section	I									
Station	1		2		3		4		Average
	ind/m²	%	ind/m²	%	ind/m²	%	ind/m²	%	ind/m² %
Chironomidae (larvae+pupae) ...	1580	81	1440	82	2380	78	1550	90	1740 82
Oligochaeta	360	18	240	14	630	21	160	9	350 16
Chaoborus	20	1	—	—	<10	<1	10	<1	<10 <1
Hydracarina	<10	1	50	3	20	<1	<10	<1	20 1
Pisidium	—	—	20	1	<10	<1	—	—	<10 <1
Big crustaceans	—	—	—	—	—	—	—	—	— —
Total fauna	1960±250		1750±320		3050±500		1730±400		2130 —
Biomass g/m²	3.3±1.8		2.8±0.6		6.2±1.8		2.4±0.9		3.7 —
Chironomid larvae:									
Tanypodinae	1210	77	1070	82	1410	64	910	60	1150 70
Chironomus salinarus-type	—	—	—	—	—	—	<10	<1	<10 <1
C. plumosus-type	190	12	170	13	730	33	200	13	320 20
Chironomini, others	160	10	60	4	60	3	380	25	170 10
Tanytarsini	10	<1	<10	<1	<10	<1	<10	<1	<10 <1

groups and biomass of the total fauna. 95 % confidence limits.

	II												III						
14		15		16		17		18		Average		19		20		21		Average	
ind/m²	%	ind/m²	%	ind/m²	%	ind/m²	%	ind/m²	%	ind/m²	%	ind/m²	%	ind/m²	%	ind/m²	%	ind/m²	%
1800	74	1500	69	1930	75	1800	76	1720	67	1750	73	1610	80	1700	53	1860	53	1720	60
550	23	640	30	610	24	540	23	770	30	620	26	330	16	1330	42	1490	43	1050	36
20	<1	20	<1	20	<1	—	--	40	2	20	<1	30	2	140	4	140	4	100	3
—	—	10	<1	<10	<1	<10	<1	20	<1	<10	<1	20	<1	—	--	—	—	<10	<1
50	2	—	—	<10	<1	—	--	—	—	10	<1	20	1	—	—	—	—	<10	<1
2420±600		2160±490		2580±880		2350±410		2550±660		2400	—	2010±450		3170±890		3490±390		2890	—
9.1±3.1		5.7±2.4		9.3±3.3		8.0±1.2		6.9±3.1		7.8	—	5.4±1.3		9.5±4.5		9.0±1.1		8.0	—
1110	63	760	52	800	43	830	46	530	31	810	47	510	32	680	41	770	42	650	38
480	27	600	41	930	50	870	48	1140	66	800	46	1030	64	780	48	1000	54	940	55
80	4	50	3	70	4	50	3	30	2	60	3	—	—	100	6	50	2	50	3
110	6	60	4	50	3	60	3	<10	<1	60	3	50	3	80	5	40	2	60	4
<10	<1	—	—	--	—	—	—	<10	<1	<10	<1	<10	<1	—	—	—	—	<10	<1

constituted about 20—25 % of the fauna. The seasonal variation of the bottom fauna is characterized by a lower part of chironomids in February, March and October as it appears from Fig. 4 b. In Västerås Bay the change in balance greatly exceeded what is likely to be a natural seasonal variation, and the oligochaetes reached about 70 % of the total number of organisms in October 1970 (Fig. 4 a).

The general change in balance between chironomids and oligochaetes coincides with the higher amounts of cooling water discharges during the

groups and biomass of the total fauna. 95 % confidence limits.

	II						III					
5		6		Average		7		8		Average	
ind/m²	%	ind/m²	%	ind/m²	%	ind/m²	%	ind/m²	%	ind/m²	%
1320	90	1400	87	1360	88	1560	95	1420	87	1490	91
130	9	140	9	140	9	50	3	90	6	70	4
—	--	30	2	20	<1	10	<1	20	1	20	1
<10	<1	30	2	20	1	10	<1	20	1	20	1
<10	<1	10	<1	<10	<1	<10	<1	<10	<1	<10	<1
<10	<1	—	—	<10	<1	<10	<1	80	5	40	2
1470±260		1610±250		1540	—	1650±310		1630±260		1640	—
1.9±0 6		2.7±1.0		2.3	—	1.8±0.9		2.3±0.5		2.1	—
980	77	1240	90	1110	83	790	53	1250	91	1020	71
<10	<1	—	—	<10	<1	—	--	<10	<1	<10	<1
50	4	20	1	40	3	30	2	<10	<1	20	1
180	14	90	7	140	10	100	7	50	4	80	5
50	4	30	2	40	3	570	38	60	5	320	22

Table 3. The bottom fauna near Aroskraft power station. Abundance of the main animal groups and biomass of the total fauna.

| Time | Sta-tion | Abundance, ind/m^2 | | | | | | | | Biomass of total fauna | | |
| | | Chironomidae | | | | Oligochaeta | | | | | | |
		Aver-age	Max	Min	%	Aver-age	Max	Min	%	Aver-age	Max	Min
July 1969	1	1530	1820	1160	79	360	530	230	18	3.3	5.0	2.5
February 1970 ...	101	340	570	40	18	1460	2430	490	79	2.5	3.7	1.3
	102	1070	1520	760	41	1400	1780	1140	54	12.9	15.1	9.5
	103	390	760	150	42	430	640	230	46	8.3	15.8	4.1
	104	170	340	80	19	680	990	380	74	2.1	3.9	1.3
March 1970	—	645± 260[1]	—		34	1130± 290[1]	—		59	11.1± 4.5[1]	—	
October 1970	—	740	1110	340	24	2130	3600	530	68	17.3	25.5	11.9

[1] 95 % confidence limits.

summer of 1969 onwards, and a correlation is plausible. The understanding of the mechanism behind the change in the benthic community demands a deeper knowledge of the chemical and microbiological conditions in the contact zone between water and bottom sediments. It might be assumed, however, that the sediment feeding oligochaetes are favoured by a higher bacterial activity caused by the temperature rise.

The most remarkable feature of the bottom fauna outside the warm water effluent is the presence of an exotic oligochaete, *Branchiura sowerbyi* BEDDARD. This species is known from Asia, Africa and Australia (STEPHENSON 1930, BRINKHURST 1966). It has been found also in some places in Europe and North America, often in artificially heated basins, but sometimes also in natural habitats (BRINKHURST *et al.* 1968, MANN 1965). A few individuals were found on station 1 in July 1969 and since then the species has increased in number in the area (Tab. 4).

Branchiura sowerbyi is by far the biggest oligochaet in the area. A specimen taken in October 1970 measured about 7 cm although it was partly fragmented. In its natural habitat the species ranges up to 15 cm (STEPHENSON *op.cit.*).

Special part

A. *Chironomidae*

A total of 41 chironomid species have been recorded as imagines from the investigated area. The distribution of the different groups within the family show a marked dominance for *Chironomini* with 21 species=51 %, while *Tanypodinae* and *Orthocladiinae* each are represented by 7 species=17 % and *Tanytarsini* 6 species or 15 %.
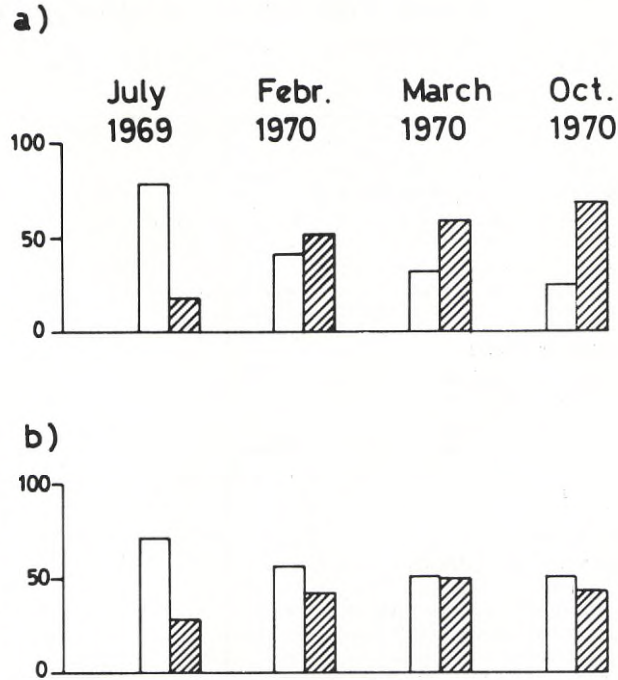
a)

b)

Fig. 4. Abundance of chirono-
mids (white) and oligochae-
tes (striped) as percentage
of the total fauna. a) Near
the effluent from Aroskraft
power station. b) In Svinne-
garn Bay.

The composition of the chironomid fauna is interesting with regard to the temperature conditions and some of the species should be further commented on:

Xenopelopia nigricans FITTKAU. Johannisberg, 20.IX.70, 1 ♂. *X. nigricans* differs from *X. falcigera* (KIEFF.) FITTKAU by the form of the hypopygial coxite lobus. It has been reported from southern Sweden by BRUNDIN (1949, *Ablabesmyia falcigera*). On the ecology of the genus FITTKAU (1962) writes: "Die Larven leben in verschiedenartigen Kleingewässern und im litoral eutropher Seen. Aus ihrem ökologischen Verhalten und ihrer Verbreitung darf man auf einen weitgehend thermophilen Character dieser Gattung schliessen."

Table 4. Occurrence of *Branchiura sowerbyi* near the warm water discharge from Aroskraft power station.

	Abundance, ind/m²			Constancy, %
	Average	Max	Min	
July 1969	11	19	0	30
February 1970 ..	76	152	0	80
March 1970	68	—	—	—
October 1970 ...	576	1023	152	100

Table 5. *Chironomidae*. Imagines along the shore line.

	June		July		September	
	I	III	I	II	I	III
Tanypodinae:						
Conchapelopia melanops MEIG.	—	×	—	—	—	—
Procladius choreus GOETGH.	—	—	×	—	—	—
P. imicola KIEFF.	×	—	—	—	—	—
P. sp. I	×	—	—	—	—	—
P. sp. III	—	—	×	—	—	—
P. sp. IV	—	×	—	—	—	—
Xenopelopia nigricans FITTKAU	—	—	—	—	×	—
Orthocladiinae:						
Cricitopus albiforceps KIEFF.	—	—	×	—	—	—
C. bicinctus MEIG.	—	—	×	—	—	—
C. bituberculatus GOETGH.	—	—	×	—	—	—
C. sylvestris FABR. incl. var. ornatus	—	—	×	—	—	×
C. intersectus STAEG.[1]	—	—	—	—	×	×
C. triannulatus McQ.	—	—	×	×	×	×
Chironomini:						
Chironomus anthracinus ZETT.	×	×	—	—	—	—
C. plumosus L.	—	×	×	×	—	—
C. thummi thummi (KIEFF.) Str.	—	—	—	—	×	×
Cryptochironomus albofasciatus STAEG.	—	—	—	—	—	×
C. rostratus KIEFF.	—	—	—	×	—	—
Endochironomus intextus EDW.	—	×	—	—	—	—
Glyptotendipes pallens MEIG.	—	—	×	×	—	—
Harnischia pseudosimplex GOETGH.	—	—	×	—	—	—
Lenzia flavipes MEIG.	—	—	—	—	×	—
Limnochironomus nervosus STAEG.	—	—	×	—	—	—
Microtendipes pedellus DE GEER.	—	—	—	×	—	—
Parachironomus arcuatus GOETGH.	—	—	×	—	—	×
P. longiforceps KIEFF.	—	—	×	—	—	—
P. biannulatus STAEG.	—	—	—	—	—	×
P. sp.	—	—	×	—	—	—
Paralauterborniella nigrohalteralis MALL.	—	—	×	—	—	—
Pentapedilum sordens v. d. VULP.	—	—	—	—	—	×
Polypedilum bicrenatum KIEFF.	—	—	—	×	—	—
P. convictum EDW.	—	—	—	—	×	—
P. nubeculosum MEIG.	—	—	—	×	—	—
Stenochironomus gibbus FABR.	—	—	—	×	—	—
Tanytarsini:						
Cladotanytarsus atridorsum (KIEFF.) EDW.	—	×	×	×	—	—
C. mancus EDW.	—	×	—	×	—	×
Tanytarsus reflexens EDW.	—	—	—	×	—	—
T. signatus v. d. VULP.	×	×	×	×	—	—
T. smolandicus BRUND.	—	—	×	—	—	—

Trissocladius grandis KIEFF. Västerås harbour, 4.V.70.
Stempellina bausei EDW. On the boat, 16.VII.69.

[1] det. Hirvenoja.

Chironomus salinarius-type. This larval type occurs frequently on the deeper bottoms of the area investigated. It is characterized by the absence of both lateral and ventral tubuli. *Chironomus salinarius* KIEFF. has not been found as imago and it is doubtful if the larvae are connected with this

species, which is a brackish water form. Quite remarkable is the occurrence of *Chironomus thummi thummi* (KIEFF.) Str. and *Chironomus anthracinus* ZETT. in view of the total absence of the *thummi*-type in the larval material investigated. It might be suggested that *C. thummi thummi* or *C. anthracinus*, or both, emanate from larvae of the *salinarius*-type, which is identical to *thummi*-larvae with their ventral tubuli reduced by environmental influence.

Chironomus thummi thummi (KIEFF.) Str. Johannisberg 20.IX.70, swarming in large number; Fullerö, 20.IX.70, 1 ♂. STRENZKE distinguishes the two subspecies *thummi* and *piger* within *C. thummi*. While *C. thummi piger* is an inhabitant of eutrophic small waters in North Germany, *C. thummi thummi* is characterized as an "Abwasserform" (STRENZKE 1959, 1960). The species has not been reported from Sweden earlier.

Cryptochironomus albofasciatus STAEG. Fullerö 20.IX.70, 2 ♂♂, one with female characters on the antennae and infected by a mermithid (*cf.* WÜLKER 1961). In Lake Constance this species is a littoral dweller found in the more polluted areas (REISS 1968). In Sweden it has been reported only from Bodsjön in Jämtland (BRUNDIN *op.cit.*).

Parachironomus biannulatus STAEG. Fullerö 20.IX.70, 1 ♂. The hypopygial characters and the colour patterns of the legs agree fairly well with the descriptions by GOETGHEBUER (1937—1938) and EDWARDS (1929). This species has not been reported from Sweden earlier but is known from England, Germany, Holland, Belgium and Finland (REISS 1968).

Parachironomus longiforceps KIEFF. Johannesberg 27.VII.70, 2 ♂♂. The distinct characters of the hypopygium makes the determination clear. The species has not been reported from Sweden earlier. The European range of *P. longiforceps* includes England, Belgium, Holland, Germany, Austria and Rumania (REISS *op.cit.*).

Tanytarsus reflexens EDW. Ekhagen 27.VII.70, 2 ♂♂. This species is easily recognized by the remarkable appendages on the anal point of the hypopygium. It seems to be quite rare, and has been found only in England, Scotland and Wales (EDWARDS 1929) and in Sweden (Lake Vättern, BRUNDIN 1949).

Tanytarsus smolandicus BRUND. Ekhagen, 27.VII.70, 1 ♂. This species is separated from *T. eminulus* (WALK.) BRUND. on the form of appendage 2 a on the hypopygium, which carries 2 lamellar, distally rounded hairs (Fig. 102 a, BRUNDIN 1947). *T. smolandicus* was described from south Sweden by BRUNDIN and it is uncertain whether the records of *T. eminulus* from England and Belgium refer to *T. eminulus* sensu BRUNDIN (*cf.* BRUNDIN 1949).

The following principal features of the chironomid fauna of Västerås Bay can be outlined:

1. The fauna is made up of eurythermal and euroxybiontic species. Littoral forms, often living inside or on the macrophytes at the shore are dominating,

e.g. Conchapelopia melanops, Endochironomus intextus, Glyptotendipes pallens, Lenzia flavipes, Limnochironomus nervosus, Parachironomus arcuatus, Pentapedilum sordens, Stenochironomus gibbus and most of the *Cricotopus* species. Among the species with an eurybath distribution are *Procladius spp., Chironomus anthracinus, C. plumosus, Microtendipes pedellus, Polypedilum nubeculosum, Cladotanytarsus mancus, Stempellina bausei* and *Tanytarsus signatus* (BRUNDIN 1949, REISS 1968).

2. The presence of three species new to Sweden and three species previously found only at single occasions is remarkable in view of the extensive studies that have been made on the chironomids of central Sweden (BRUNDIN 1949, SANDBERG 1969).

Some of the species found, *e.g. Chironomus thummi thummi, Parachironomus biannulatus* and *Parachironomus longiforceps,* can be regarded as southern elements in the Swedish chironomid fauna and there might be a connection between the discharges of cooling water and the presence of species with a southern geographical range.

3. Many of the species identified — about 32 % — are also reported from brackish water habitats. Among these are *Cricotopus triannulatus, Chironomus plumosus, Glyptotendipes pallens, Harnischia pseudosimplex, Lenzia flavipes, Leptochironomus tener, Limnochironomus nervosus, Microtendipes pedellus, Parachironomus biannulatus, Polypedilum bicrenatum, Polypedilum nubeculosum,* and *Cladotanytarsus mancus* (BRUNDIN 1949, PALMÉN 1955, THIENEMANN 1954, HIRVENOJA 1962 and REISS 1968).

This is perhaps not specific for the area here concerned, but a general phenomenon of highly eutrophic waters, and connected with the physiological adaptability of the organisms. STRENZKE (1960) mentions that the respiratory intensity is connected generally with the osmotic pressure of the body fluids. It is possible that some species because of their osmotic configuration are able to stand a certain salinity as well as a generally low oxygen pressure of the environment.

B. *Oligochaeta*

Some of the oligochaete material has been kindly analysed by Dr GÖRAN MILBRINK, (Institute of Freshwater Research, Drottningholm). He writes:

"As a rule tubificid species are valuable indicators of pollution when occuring in characteristic tubificid communities, seldom as isolated species.

The northern part of Västerås Bay is characterized by large numbers of the tubificids *Limnodrilus hoffmeisteri* CLAPARÈDE and *Potamothrix hammoniensis* MICHAELSEN implying severe conditions for animal life. This specific composition of tubificids is wellknown for instance from one of the most polluted parts of Lake Vänern, close to the city of Karlstad, and from Galten similarly one of the most polluted basins of Lake Mälaren.

Table 6. Abundance of the most important animal groups in 1913—1915 and 1969, ind/m².

	Autumn		Early summer	
	September 1913 (12 m)	October 1969 (15 m)	June 1915 (12 m)	July 1969 (10 m)
Pontoporeia affinis	340	—	250	—
Chironomidae	10	1930	50	1740
Oligochaeta	120	300	310	620

L. hoffmeisteri is in dominance close to the city of Västerås, while *P. hammoniensis* becomes more and more important at a further distance from the city.

The distribution of the warm water tubificid *Branchiura sowerbyi* BEDDARD is supposed to be limited to the warm water effluent near the harbour of Västerås. (*Cf.* page 206).

Aulodrilus pluriseta PIGUET, *Limnodrilus claparedeanus* RATZEL, *Limnodrilus udekemianus,* and *Tubifex tubifex* MÜLLER — all tolerant species — are scarce in Västerås Bay as well as in Ridö Bay situated to the south of the former.

The dominant species in Ridö Bay is *P. hammoniensis. L. hoffmeisteri* is of less importance. The species composition indicates a lower degree of pollution than in the northern part of Västerås Bay."

C. *Lamellibranchiata*

The very sparse representation of the genus *Pisidium* has already been pointed out. Only three species have been found. The most frequent is *Pisidium moitessierianum* PALADILHE, which occurs at all depths in the area. *P. moitessierianum* is found on many localities in the remainder of Lake Mälaren, down to a depth of 15 metres. According to ELLIS (1962) it is a calcicole species and does not live in soft waters. It is reported by ODHNER (1940) from different parts of Sweden. *Pisidium henslowanum* SHEPPARD occurs at a few stations in the area. It is known to inhabit streams, rivers, canals, marsh drains, lakes and ponds, particularly in running water (ELLIS *op.cit.*). A few specimens of *Pisidium casertanum* POLI were found in Fullerö Bay at a depth of 10 to 15 metres. It is recorded from all kinds of habitats (ELLIS *op.cit.*) and occurs frequently in the whole of Lake Mälaren down to 50 metres (WIEDERHOLM unpublished material). Scattered findings of *Anodonta sp.* have been made at a depth of 4 metres. A remarkable feature is the total absence of *Dreissena polymorpha* PALLAS, which is extremely abundant in the northern part of Lake Mälaren (WIEDERHOLM 1970).

IV. Comparison with earlier investigations

Through the investigations of ROSÉN (1915) and ALM (1927) we have some information on the development of the bottom fauna of Lake Mälaren during the last 55 years.

It appears that a drastic change in the composition of the macrobenthos has taken place since the beginning of the century (Tab. 6). The relict crustacean *Pontoporeia affinis* was frequently represented in the whole area in 1913—1915, but is nowadays totally absent with the exception of a few individuals in the shallow outer parts of Västerås Bay. It is also clear, that the chironomids have increased considerably while the change in oligochaete abundance is uncertain because of somewhat different sampling techniques.

Generally the results illustrate an extensive change in the benthic environment and a considerable rise of the trophic level of the whole basin.

V. Conclusions

It appears that the macrobenthos in the area is influenced strongly by human activities. A rich supply of organic material to the sediments maintains a large biomass, and the fauna is composed of organisms with a high ability to resist periods of oxygen deficit of the bottom water. The severe conditions are stressed by the observation of dense swarms of *Chironomus thummi thummi,* known as a sewage water species.

The inner part of Västerås Bay is characterized by the absence of filtering organisms. Instead the fauna is composed of sediment feeding or predatory forms as oligochaetes, tanypodins, *Cryptochironomus* species and *Chaoborus* larvae. These organisms are able to exploit water layers close to the bottom for their respiration and are not affected immediately by oxygen deficit in the contact zone between water and sediment. Thus the oligochaetes bring about a water circulation through ondulating movements with the hind part of their body, while the predatory forms are able to leave the critical zone temporarily for their oxygen uptake.

At some distance from Västerås the conditions are improved. A well developed *Chironomus* fauna, supported by the high supply of detritus to the sediments, is found in sections II and III.

The effect of cooling water discharges on the *quantitative* development of the bottom fauna within the basin on a large scale can not, with the information now available, be separated from the effect of the general eutrophication. However, a rise of the biomass seems to be at hand near the effluents, essentially because of the large numbers of oligochaetes. This is supposed to be a result of a temperature stimulation of the microbiological activities in the ooze which favours the sediment feeding oligochaetes.

The *qualitative* features of the fauna indicate a temperature influence in the whole area studied. The presence of southern chironomid species is supposed to be a result of a rise in temperature which enables these species to pass through their development from larvae to imagines on a more northern latitude than their natural habitat ranges.

VI. Summary

1. The bottom fauna of a basin of Lake Mälaren has been investigated, especially with regard to the effects of cooling water discharges.
2. The composition of the total fauna reflects a pollution gradient from the town of Västerås towards the main part of Lake Mälaren.
3. A larger biomass is noted near the warm water discharges, principally because of higher abundance of oligochaetes. The warm water tubificid *Branchiura sowerbyi* is found near an effluent.
4. Three chironomid species new to Sweden are recorded. It is suggested that the composition of the chironomid fauna reflects a temperature influence in the whole basin.

VII. Acknowledgments

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