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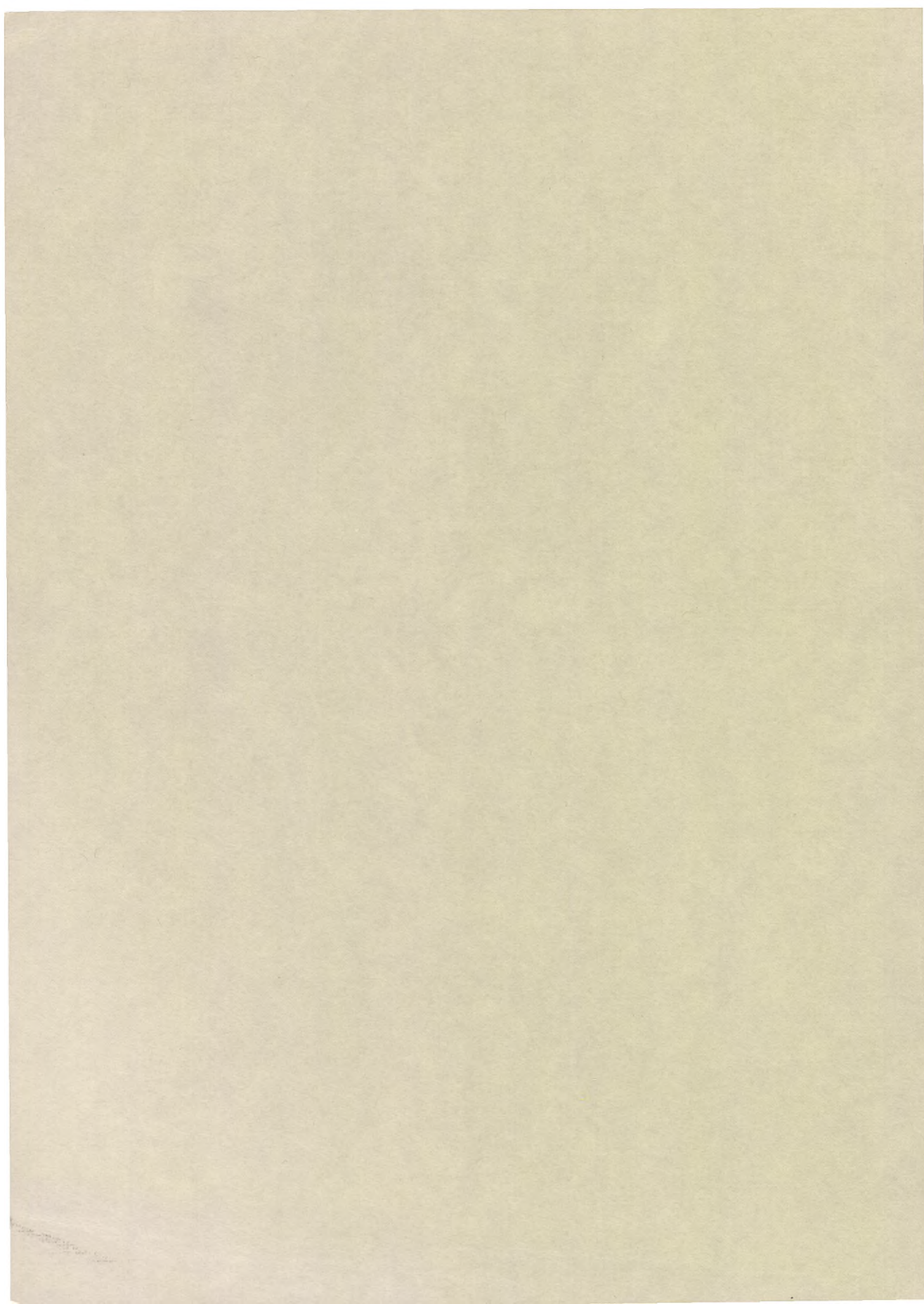


INSTITUTE OF FRESHWATER RESEARCH

DROTTHINGHOLM

Report No 53

LUND 1973
CARL BLOMS BOKTRYCKERI A.-B.



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The Hatching, Distribution, Abundance, Growth, and Food of the Larval Lake Whitefish (*Coregonus clupeaformis* MITCHILL) of Central Green Bay, Lake Michigan

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I. INTRODUCTION

The lake whitefish (*Coregonus clupeaformis* MITCHILL) has been one of the principal commercial fishes of the St. Lawrence Great Lakes. Numerous papers have been published on the adults of this fish, but very little has been published on the young in nature. This study represents only the fourth contribution on wild larvae in North America, and the first on the Lake Michigan stock. This study was performed in Central Green Bay and adjacent Lake Michigan (Fig. 1) because it has remained a productive whitefish area.

In all of the Great Lakes the whitefish has experienced extreme fluctuations in abundance. Reasons for most fluctuations remain unclear although several attempts have been made to correlate weather patterns, intensity of the fishery water levels and interspecific relationships with year class success (CHRISTIE, 1963; LAWLER, 1965; DOAN, 1942). Year class strength for whitefish is determined in the first couple months of life, and perhaps the first three weeks after hatching. Thus the larvae stage, which should have received most attention, is the most important but has been sorely neglected in Great Lakes research.

This study provides basic information on larval whitefish distribution, development, times of hatching, movement, feeding, yolk-sac conversion, densities, growth, and interspecific relationships. In essence it summarizes the entire findings from the field.

Part II of this study (HOAGMAN, 1973) re-

presents the laboratory phase of the program. Larval whitefish, captured in the field, were reared in a large environmental chamber. Experiments were performed on swimming speed, phototaxis, rate of digestion, time to starvation, temperature preference, growth rate determined and general behavior observed.

II. MATERIALS AND METHODS

Larval whitefish were captured with 50 cm (diameter) plankton nets with 1.76 m bags towed from small boats with booms perpendicular to the gunwale. The mesh of the nets and terminal bucket was number 0 (zero) which for the nylon material has 0.569 mm openings.

A unit of effort was defined as a five-minute tow with one net at 0.805 m/sec (1.8 mph). Results are presented as average catch per unit of effort (CPE). Tows were made with the net at the surface and unless specifically stated otherwise, a tow means a five-minute surface tow.

In areas where larvae could be captured attempts were made to sample day and night for each date. Day collections were taken from 1200 to 1800 hours (CST) and night sampling began at dusk and continued to 2400 hours. After each tow, the larvae were counted and preserved in 10 % formalin.

From all larvae collected in 1968 and 1969, and selected dates and locations in 1970, laboratory analyses were made of 50 preserved specimens by date to determine total length, size of yolk-sac, development, and stomach contents. Total length and length of yolk-sac were measured to the nearest 0.1 mm under a microscope.

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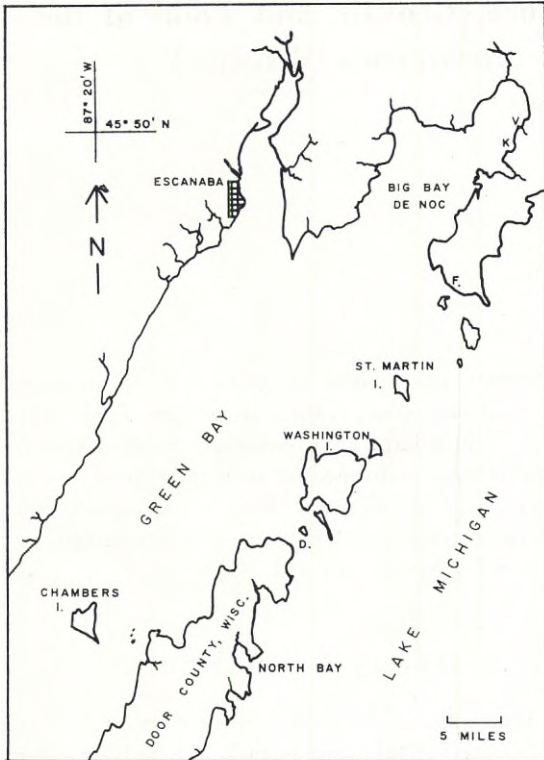


Fig. 1. Simplified chart of study area. Valentines and Kates Bay indicated by V and K, Fairport by F, and Deaths Door by D. Menominee is just SW of Chambers Island.

In 1970 attempts were made to discover the direction and speed of the currents in central Green Bay and adjacent Lake Michigan. Drogues were constructed of sheet aluminum in the shape of a 5° frustrum, 46 cm in diameter by 30 cm high with wooden cross partitions 7.6 cm deep. Similar drogues were found suitable for detecting currents in the Great Lakes by CSANADY, 1964. Surface currents were also measured with fluorescein dye contained in cheesecloth bags tied to anchored buoys. For both the dye and drogues, current speeds were calculated by measuring the distance they had moved from a reference buoy in a known interval.

Three stations were selected for weekly sampling and provided the most specimens for this study. These three stations were designated as "index" stations (Fig. 2), and are indicated by B-3, M-3, M-4.

Description of Index Stations

The three index stations differ markedly in their physical characteristics. B-3 along the east shore of Chambers Island and M-4 (North Bay) are nursery areas, whereas M-3 and Kates Bay (in Big Bay de Noc) are spawning areas. The larvae at these stations seem dependent on two primary physical parameters, water temperature and currents. Each area has the following characteristics. B-3 extends 5446 m along the east shore of Chambers Island, and is 100 m wide beginning at the waters edge. The water is clear, free of aquatic vegetation and the bottom is rubble and some sand. The depth ranges from 0 to 2 m. The entire area is protected to some extent by a large shallow shelf 1.6—2.4 km from the east shore of Chambers Island (Fig. 2) which acts to drive south running currents away from the east shore. During northerly winds large waves pound the east shore and the water becomes very turbid. During south, southwest, west, or northwest winds, B-3 is usually calm or at most choppy.

North Bay (M-4) is a shallow, well protected bay of Lake Michigan. Approximately $\frac{1}{2}$ the bay is less than 1.5 m deep. The bottom is primarily sand with rocks only as scattered patches and near the mouth. Emergent aquatics (*Scirpus* and *Typhus*) grow dense in the shallowest areas along the northwest rim and as isolated beds away from shore. Strong winds regardless of direction do not cause heavy seas in North Bay, nor do heavy seas penetrate from Lake Michigan. Wind stress over Lake Michigan often causes water level variations in North Bay. Southerly winds force water into the Bay and northerly winds lower the water. In winter, North Bay is locked in ice.

M-3 is a strip of water 100 m wide just south of North Bay. It extends from the southern tip of North Bay to the first shore indentation 2.1 km south (Fig. 2). Here the shore is composed of large slabs of rock, massive boulders, and rock shelves that extend underwater into the sampling area. The bottom of the entire sampling area is almost solid rock. The depth along the inner edge of the strip is 0.5 to 1 m and the outer edge 3 to 5 m. The bottom outside of M-3 is also rock with occasional patches of firm clay. M-3 is subject to violent wave action and strong shore currents. The

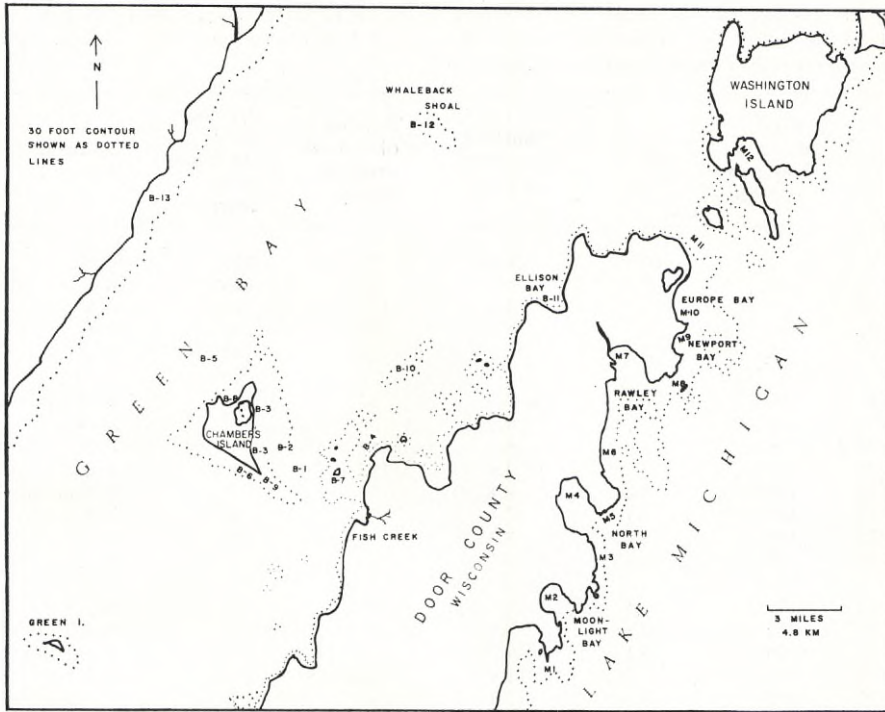


Fig. 2. Stations in Green Bay and Lake Michigan where currents were measured and tows made for larval

whitefish. Thirty foot (9.1 m) contour shown as dotted lines.

lake whitefish spawns at depths of 4 to 15 m along M-3. These depths occur at distances beyond the winter ice cover along shore.

None of the index stations border zones of permanent human habitation and even the summer cottages are few. References should be made to U.S. Lake Survey charts numbers 701 and 702 for full details of depths, bottom types, shore configurations, and other features not specifically mentioned above and for areas sampled but not described.

Water Currents

Water currents along the shore at B-3 and M-3 flow parallel to the shore in the direction of the prevailing wind. At M-3 south running currents varied from 5.3 to 9.6 cm/sec (Table 1). Typical surface water speeds at B-3 varied 4.8 to 7.8 cm/sec. A north to northeast wind creates a strong current between the east shelf of Chambers Island and the island complex east of Chambers Island. Some of this water turns westward at B-2 and flows di-

rectly to Chambers Island where some of it passes over Hanover Shoal (B-9) and some counteracts the southerly flow moving along the east side of Chambers Island (Table 1, 4/25/70). During southerly or westerly wind there is little water movement along the east side of Chambers Islands.

The pattern of water movement in North Bay was not measured, but information supplied by a local resort owner and two fishermen who fish there every weekend provides the general pattern. They all said that under a southerly wind the water rotates counterclockwise and under a northerly wind it rotates clockwise. The morphometry and position of North Bay relative to Lake Michigan and its shore currents, tends to indicate that this should occur. With either a north or south running current along the eastern Door County shore, some Lake Michigan water would be carried into North Bay. A north running current would probably have the greatest effect. North running currents would carry water from M-3 to North Bay and south running currents would carry water

Table 1. Average current speeds and direction measured in Green Bay, Lake Michigan. Data from drogues set at the surface and 0.5 m or 0.5 m and 1 m. Correction factor of 0.71 applied. Currents grouped by sector wind was blowing to.

Date	Wind direction going to in degrees	Wind speed, m/sec	Surface current, cm/sec	Bearing of drogues, degrees	Previous wind (24 hours prior) degrees	Location (Figure 2)
4/ 5/70	0	10.3	24.9 ¹	25	113	M-1
4/25/70	40	2.6	6.7	60	45	B-4
5/ 2/70	0	1.0	4.8	145	40	B-3
5/ 2/70	30	3.1	4.4	235	40	B-5
4/ 3/70	25	2.6	26.4 ¹	20	140	M-8
4/ 4/70	90	6.2	7.5	52	237	M-3
4/ 4/70	113	6.0	9.2	65	237	M-5
4/17/70	90	4.6	5.1	112	45	B-1
4/17/70	157	3.9	2.4	192	45	B-2
4/17/70	157	3.2	6.1	165	45	B-3(south)
4/17/70	180	4.1	7.1	180	45	B-3(north)
5/ 8/70	135	2.6	5.3	50	225	M-3
5/16/70	150	6.1	4.5	185		B-12
4/10/70	225	6.5	9.6	195	135	M-3
4/11/70	270	0.8	3.5	221	250	M-8
4/12/70	215	5.1	9.7	196	270	B-2(21 m)
4/12/70	215	7.2	11.4	110	270	B-2(5 m)
4/18/70	240	3.5	10.1	233	135	M-5(3 m)
4/18/70	248	4.6	11.5	210	135	M-5(16 m)
4/18/70	240	3.5	7.2	185	135	M-3
4/19/70	235	11.1	7.1	42	240	B-14
4/25/70	210	1.6	2.5	7	calm	B-2
4/25/70	210	2.1	5.4	10	calm	B-3
4/25/70	210	3.1	1.0	279	calm	B-1
5/ 9/70	270	2.6	10.5	156	200	M-11
5/ 9/70	270	2.5	9.2	185	200	M-10(north)
5/ 9/70	270	2.5	5.1	180	200	M-10(middle)
5/ 9/70	270	2.5	2.3	160	200	M-10(south)
5/ 9/70	270	2.5	5.6	180	200	M-9
5/23/70	180	3.8	2.6	245	225	B-1
5/23/70	180	3.1	6.4	200	225	B-2
5/23/70	180	3.8	7.8	191	225	B-3
5/24/70	225	3.1	8.0	10	180	M-3
5/ 3/70	320	3.1	7.2	355	0	M-3
5/ 4/70	325	2.6	3.4	309	320	M-11

¹ Velocities calculated by triangulation method using shore objects and buoys. Probably in error.

from M-5 (a minor spawning area) to North Bay and also entrain some water from the northern edge of M-3.

According to C. H. MORTIMER (personal communication)¹ a steady 8 m/sec wind blowing down the long axis of Green Bay sets up, after 40 hours, the following currents patterns pertinent to this

¹ Director, Center for Great Lakes Studies, The University of Wisconsin-Milwaukee.

study: (1) a strong current out of Death's Door (M-11) which then flows south along the Door Peninsula; (2) strong currents entering northern Green Bay just south of the Garden Peninsula which turn north and sweep along the east edge of Big Bay de Noc (Valentines and Kates Bay area), this water then flows along the west shore of Big Bay de Noc, across northern Green Bay and then down the west shore of central Green

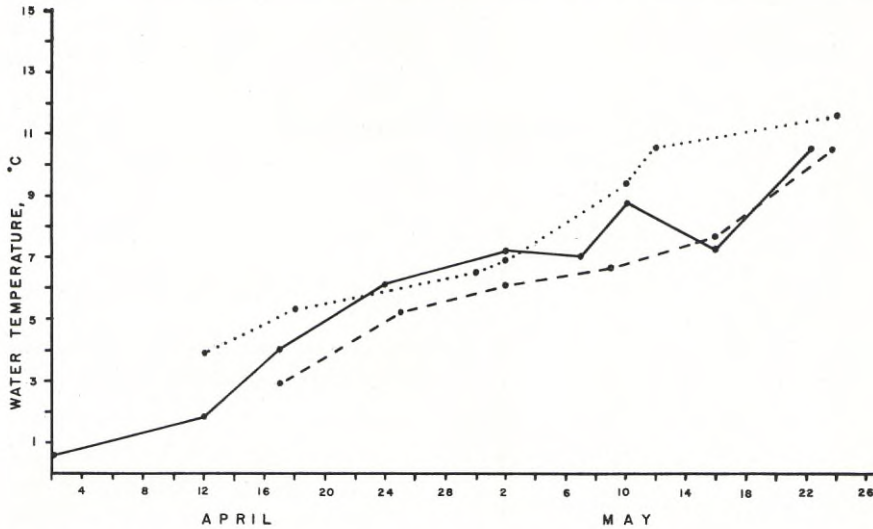


Fig. 3. Surface water temperatures along the east side of Chambers Island (B-3) in 1968 (dotted), 1969 (dashed), and 1970 (solid) during April and May.

Bay past Chambers Island; (3) from Death's Door south to Chambers Island occurs a zone of much turbulence and cross currents and some of the northern water is diverted out of Death's Door. For a steady wind of 8 m/sec blowing up (to northeast) the long axis of Green Bay, MORTIMER predicts: (1) water should flow north along the eastern shore of Door County and most of it turns northward after passing through Deaths' Door; (2) some of this water turns southward toward Chambers Island but seems to miss it along the west side; (3) the flushing of Big Bay de Noc is opposite to the north wind and the water that passes along the east shore flows out into the Lake Michigan past St. Martins Island and between Fairport and Summer Island.

Water Temperatures

The three springs were dissimilar in the warming of the water near Chambers Island and at selected water intakes. The spring of 1968 was the earliest and warmest, 1969 the coolest and latest, and 1970 intermediate between the previous two (Table 2). Water temperatures equivalent to 1968 occurred two to three weeks later in 1969 during the period March through May. The water temperatures of B-3 reflect the same pattern of warming (Fig. 3).

For all years the water temperature at B-3 had risen to 6.0 C by May 1 (Table 3). In 1969 and 1970 the water temperature rose only to 8.0 C by May 18, but in 1968 it was approximately 11.0 C by this date.

On April 3 and 10, 1970, the temperature was 1.8 and 2.5 C at M-3 and the water column was homothermous to depths of 35 m offshore (Table 3). By the first week of May, however, M-3 surface temperatures were 2 to 4 C higher than bottom temperatures at 27 m. M-3 water reached 6.0 C by April 22, 1970. The warm water of 10.2 and 9.7 C on May 4 and 8, 1970 at M-3 was coming from North Bay because the surface waters at M-5 were only 8.3 and 8.1 C.

North Bay (M-4) always had warmer water than M-3 during the spring of 1970, usually by 2 to 3 C. In terms of spring warming, North Bay temperatures represent a 6 to 10 day advance over M-3. Temperatures throughout M-4 were 6 C by April 14, 1970, and reached 10.7 by April 26. After April 26, 1970, a long stretch of cool weather kept the M-4 temperatures nearly constant at 10.5 C until May 20. By June 6, 1970, M-4 had warmed to 20.5 C.

One would expect the shallow water of B-3 to be warmer than M-3 or M-4 on equivalent dates

Table 2. Water temperatures at Menominee and Escabana water intakes in 1968 and 1969, averaged by five-day intervals and expressed as degrees centigrade.

Date	Escabana		Menominee	
	1968	1969	1968	1969
3/20	1.8	1.5	2.9	2.2
3/25	2.1	1.6	3.3	2.5
3/30	2.8	1.7	3.7	2.2
4/ 5	3.3	2.1	4.4	2.3
4/10	3.8	2.1	5.4	2.7
4/15	4.7	2.6	7.1	3.8
4/20	5.6	3.3	7.8	5.0
4/25	5.6	3.3	7.2	5.4
4/30	6.0	5.1	7.2	6.1
5/ 5	7.8	5.7	8.9	7.6
5/10	9.3	6.1	9.4	8.7
5/15	10.6	6.7	10.5	8.6
5/20	11.1	8.3	11.1	9.4

Table 3. Surface water temperatures at index stations, Green Bay and Lake Michigan. Values are averages for areas and day, or averages of two days within area. Expressed as degrees centigrade.

Date	1968	1969	1970	1970	1970	1970
	B-3	B-3	B-3	B-1	North Bay	M-3
4/ 2	—	—	0.6 ¹	0.7 ¹	0.7 ¹	—
4/ 3	—	—	—	—	—	1.8 ²
4/10	—	—	—	—	4.8	2.5
4/12	3.9	—	1.8 ²	1.0 ²	—	—
4/17	—	2.6	4.0	2.1	—	—
4/18	5.3	—	—	—	7.0	5.1
4/19	—	—	—	2.3	—	—
4/24	—	—	6.1	3.4	—	—
4/25	—	5.2	—	—	—	—
4/26	—	—	—	—	10.7	7.0
4/30	6.5	—	—	—	—	—
5/ 2	6.9	6.1	7.2	4.0	—	—
5/ 3	—	—	—	—	10.5	—
5/ 4	—	—	—	—	—	10.2
5/ 7	—	—	7.0	6.5	—	—
5/ 8	—	—	—	—	10.6	9.7
5/ 9	—	6.7	—	—	—	—
5/10	9.4	—	8.8	6.9	—	—
5/12	10.6	—	—	—	—	—
5/16	—	7.7	7.3	5.9	9.6	7.6
5/23	—	—	10.6	9.1	—	—
5/24	—	10.5	—	—	13.5	11.0
5/30	11.9	—	—	—	—	—
6/ 6	—	—	15.7	13.0	20.5	12.7
6/10	13.4	12.3	—	—	—	—

¹ Ice over Green Bay except in small areas. Temperatures are from open water near Fish Creek and North Bay in small open area.

² Ice floating in large masses on Green Bay and small pieces at M-1.

but instead it was cooler (Table 3). The most probable reason is that B-3 was influenced more by offshore water than M-3. Along the east shore of Door County the water travels up and down the coast whereas at B-3 the coast water is often replaced by offshore water, or at least mixed with it.

III. RESULTS AND DISCUSSION

Distribution and Abundance of Larval Whitefish. Dispersal and Distribution

The distribution of larval whitefish in central Green Bay and adjacent Lake Michigan during April and May was not uniform. Over deep water, surface tows and tows to 5 m yielded few or no larvae, and surface tows over depths of 1 to 3 m near shore had great differences in CPE depending on the stations being compared. Larval whitefish were found regularly at only B-3 in central Green Bay and at M-3 and M-4 in adjacent Lake Michigan.

Fig. 4 summarizes all areas and years of collection. All of the areas indicated with a letter had 4 to 12 tows made there on at least two occasions when larval whitefish were being caught at the index stations. In Fig. 4 the divisions are, N= not caught; R="Rare," which is less than one larva per tow; and C="Common," which is one or more larvae per tow. Since all dates were considered and average CPE of each date was used, this represents the steady state condition during peak abundance from the latter part of April through the first half of May.

Larval whitefish were seldom captured over water depths greater than 3 m. Surface tows northwest of Chambers Island, between Chambers Island and the island complex on the east, south of Whaleback Shoal, in Death's Door, and beyond the 10 m contour in Lake Michigan yielded negligible numbers of larvae if any. Subsurface tows in these areas produced the same.

Water depth alone was not primary in determining larval distribution because even at depths of 1 to 3 m in areas which were seemingly identical productive areas, larvae were absent or rare. Larval whitefish were never common at Whale-

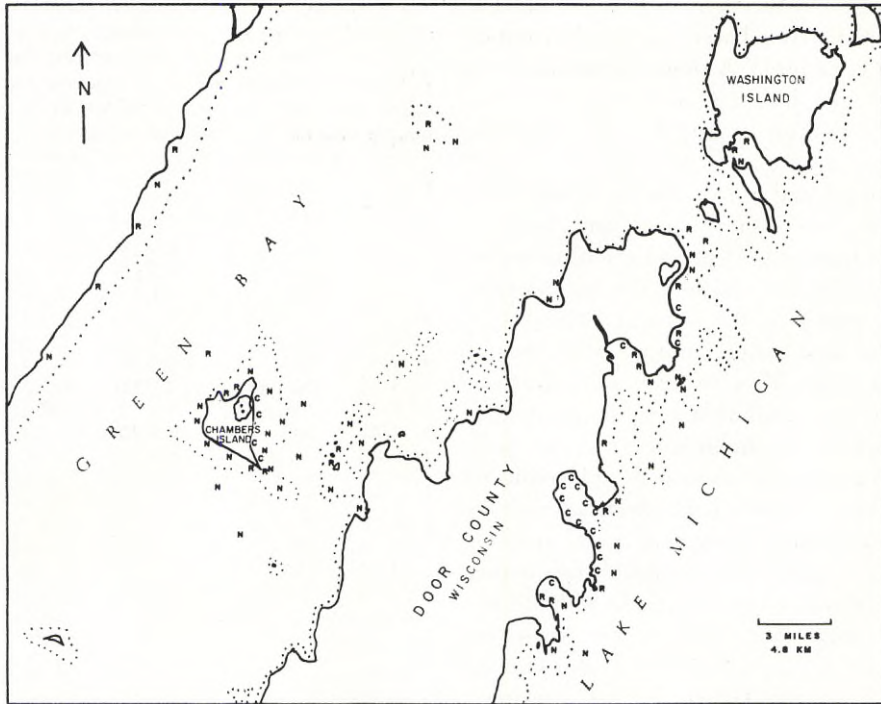


Fig. 4. Generalized abundance of larval whitefish over entire study area during the first two weeks of

May. All years of collection and day and night effort combined. N=not caught, R=rare, C=common.

back Shoal, along the west shore of Green Bay, along the west or southwest side of Chambers Island, over Hanover Shoal, around the island complex east of Chambers Island, along the east shore of Green Bay, over shoals in Lake Michigan, or near offshore islands in Lake Michigan. The best example of localized distribution in shallow water is shown by the three years of collection near Chambers Island. The east shore especially near the southeast tip, always produced larvae whereas the other side yielded larvae on only one occasion and that was near the southeast tip.

Near zones where larvae were abundant, catches dropped to zero as the depth of water increased away from shore. Usually larvae could not be found 100 to 150 m from shore if the water was greater than 3 m deep. Larvae catches in North Bay dropped to few or none in water deeper than 1 m.

In Green Bay and Lake Michigan the larvae were always caught in greatest abundance close to the surface. Towing the net 1–3 m down in

areas of larval abundance yielded few larvae. If the same area was crossed with the net at the surface, many would be captured. On only two occasions were larvae captured deeper than 2 m. In North Bay the water was often so shallow that the net had to be lifted to prevent its lower edge from digging into the sand.

This study agrees with others on larval whitefish distribution and preferences. HART (1930) found whitefish larvae in the Bay of Quinte, Lake Ontario, primarily near the surface in shallow water over a rubble bottom and over sand. FABER (1970) used a sled net to sample whitefish larvae in South Bay, Lake Huron. He towed along the bottom in water 1.3 to 4.6 m deep and found the greatest abundance at 1 to 3 m over coarse rubble along steeply sloping shores. He could not tow in shallower water. RECKAHN (1970) found young-of-the-year whitefish in water 0.3 to 1 m deep near aquatic vegetation in the same bay that Faber sampled. Reckahn reported that the initial habitat selected by the larval whitefish after

release from the hatchery was, . . . "within the edge and immediately adjacent to emergent stands of cattails (*Typha spp.*)." A similar dependence on specific areas for hatching and early life was shown by LINDSTRÖM (1967) for the whitefish species of Swedish lakes.

From my work and others, the larval whitefish prefer the shallow inshore areas and bays to depths of not more than 3 m and the distribution in such areas is highly variable. The bottom type is secondary, providing the physical influences of waves, current, and temperature allow the larvae to congregate there. They live primarily near the surface for at least their first two months of life. Such a dependence on the inshore water for early life makes the whitefish extremely vulnerable to sudden changes of this environment, as well as long-term detrimental changes in water quality.

An adequate appraisal of localized distribution of whitefish larvae can only be made with knowledge of the spawning stock and the spawning grounds. There are no known areas of whitefish spawning in central Green Bay. Commercial fishermen and biologists with the Wisconsin Department of Natural Resources, contend that the nearest spawning grounds to Chambers Island are outside Door County along the Lake Michigan shore, Little and Big Bay de Noc in northern Green Bay, and perhaps small areas of the northern Green Bay shoals.

Along the Door County shore of Lake Michigan the greatest numbers of ripe and running whitefish are taken near North Bay in late October. Numerous pound nets are scattered north and south of the North Bay mouth and gill nets are set commercially in deeper water offshore. The commercial fishermen that have fished this shore for years do not believe any substantial spawning of whitefish occurs away from the North Bay area. Biologists with the Wisconsin Department of Natural Resources believe the same.

According to commercial fishermen from the northern Green Bay region and to biologists with the Michigan Department of Natural Resources, the primary spawning grounds of the lake whitefish are along the eastern shore of Big Bay de Noc just north of the city of Garden. Valentines Bay and Kates Bay border the prime areas (Fig. 1). Large quantities of larval whitefish were captured

Table 4. *Day and night comparisons of average CPE of larval whitefish at three index stations. Collections made over same areas, number of tows in parentheses. The grand averages are the correction factors used to adjust the data on several dates when only a day sample or a night sample was taken.*

Date	Location	Day CPE	Night CPE	Ratio N/D
5/ 2/69	B-3	1.3(14)	1.9(14)	1.5
5/10/69	B-3	9.0(17)	91.5(14)	3.5
4/10/70	M-3	4.1(12)	13.5(4)	3.0
4/18/70	N. Bay	0.5(16)	6.2(8)	12.4
4/18/70	M-3	12.5 (8)	27.4 (8)	2.2
4/24/70	B-3	0.2(66)	0.4(48)	2.0
5/ 3/70	N. Bay	16.0(22)	173.0(16)	10.8
5/ 5/70	Fairport	0.5(32)	10.4(12)	20.8
5/ 7/70	B-3	5.3(20)	7.3(24)	1.4
5/ 8/70	N. Bay	5.4(16)	178.0(16)	33.0
5/ 8/70	M-3	19(28)	13.5(16)	7.1
5/16/70	B-3	4.0(42)	7.4(28)	1.9
5/16/70	N. Bay	3.3(20)	28.7(12)	8.7
5/16/70	M-3	0.4(20)	4.4(12)	11.0
5/23/70	B-3	2.0(28)	1.0(28)	0.5
5/24/70	N. Bay	0.2(16)	4.3(12)	21.5
N/D Ratio				
Average for B-3, excluding 5/23 sample				2.1
Average for M-3				4.6
Average for North Bay, Lake Michigan				17.3

from these two bays on May 6 and 7, 1970. Small numbers were captured near and east of Fairport.

Shore zones adjacent to spawning areas may act as nursery areas but this study shows that nursery areas may also be far removed. The distribution in central Green Bay can be accounted for by the strength and general nature of the currents in the northern Bay. The spawning grounds in Lake Michigan probably provide larvae for the numerous bays along eastern Door County with North Bay the major recipient. Since the larvae are random swimmers their first few weeks with maximum swimming speeds (HOAGMAN, 1973) below that of the currents measured; their existence is essentially planktonic and actual distribution is dependent on the physical forces of the area.

Abundance

The CPE for a particular area was not only related to the abundance of larvae but also to the time of day the tows were made. With one exception, night tows always yielded more larval whitefish than day tows (Table 4). The average

Table 5. Catch per unit of effort of larval whitefish in 1968-70 at index stations in Green Bay and Lake Michigan. Expressed as average for period of collection. Number of tows in parentheses.

Date	B-3, 1968		B-3, 1969		B-3, 1970		North Bay, 1970		M-3, 1970	
	Total taken	CPE	Total taken	CPE	Total taken	CPE	Total taken	CPE	Total taken	CPE
4/ 3 & 4	—	—	—	—	—	—	—	—	0	0 (16)
4/10 & 11	—	—	—	—	0	0 (34)	28	0.9 (16)	103	6.5 (16)
4/18 & 19	—	—	1	0 (15)	0	0 (24)	53	2.4 (24)	319	19.9 (16)
4/25 & 26	—	—	3	0.2 (13)	35	0.5 (112)	5135	3.2 (24)	1233	156.9 (22)
5/ 1 & 2	75	9.3 (8)	46	1.6 (28)	43	0.9 (69)	—	—	—	—
5/ 3 & 4	—	—	—	—	—	—	3117	82.5 (38)	75	13.1 (16)
5/ 7 & 8	—	—	—	—	282	6.3 (44)	2941	91.9 (32)	125	4.5 (28)
5/10 & 11	267	12.2 (21)	593	17.6 (33)	74	1.7 (62)	—	—	—	—
5/16 & 17	—	—	4	0.3 (16)	378	5.7 (70)	—	—	60	1.9 (32)
5/23 & 24	—	—	0	0 (18)	82	1.5 (56)	54	1.9 (28)	18	2.9 (16)
5/29 & 30	0	0 (18)	—	—	—	—	—	—	—	—

ratios of night CPE to day CPE for B-3, M-3, and M-4 were 2.1, 4.6, and 17.3. These values were used as correction factors to adjust the average CPE of day or night tows, when a particular date had only one or the other. NOBLE (1970) found the same day and night and depth relationship for yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum*) fry using the Miller high-speed sampler. As the whitefish larvae grew, the trend intensified.

The larvae never were as abundant at B-3 in any year as at M-3 or North Bay in 1970 (Table 5). Based on average CPE, the B-3 larvae were approximately 10% as abundant as at North Bay and M-3. At B-3 the larvae were abundant earlier in 1968 than 1969 or 1970. Both 1968 and 1969 CPE curves resemble a normal curve, but in 1970 at B-3 there were two peaks (Fig. 5), which were both lower than the previous two years. At B-3 a few larvae could be expected from April 18 to 25, but they would not arrive in large numbers until May 1. From morphological characteristics and size of yolk-sacs, the larvae arrived at B-3 from 7 to 16 days after hatching. Here they would remain approximately 2 to 3 weeks. After May 17, little success was obtained at capturing larval whitefish at B-3.

The Lake Michigan catches at M-3 and North Bay peaked earlier than in Green Bay. The CPE near the spawning grounds show the nature of the hatching interval and the time of peak hatch in 1970 (Fig. 6). Hatching was in progress to a

limited extent on April 10, increased steadily and peaked between April 22 and 30. The catches in North Bay followed the CPE's at M-3 by several days and continued well beyond the time of peak hatching. This indicates the whitefish larvae were moving into North Bay and utilizing it as a nursery area. The decline in the CPE in North Bay followed the decline at M-3 by 13 to 20 days, indicating the larvae remain in the shallow water of North Bay for 2 to 3 weeks (or more) after hatching. By late May larvae were still abundant in North Bay but not to the extent of earlier collections. A part of the reduced success in capture, was failure to sample the larvae proportionately to their abundance because of their increased size and speed.

The average CPE's at M-3 in 1970 can be used to approximate the length of the incubation period. Mature whitefish began arriving offshore of M-3 to spawn about the first of November and by November 10, spawning activity is at a maximum. Spawning is usually over by November 20.¹ Assuming all whitefish spawn on November 10 and all larvae hatch on April 20, gives an incubation period of 161 days. Since the majority of spawning was the 10 days, after November 10, and the peak hatch in 1970 was April 20 plus approximately 10 days; the best estimate for duration of incubation for the entire population is 155 to 170 days. FABER's (1970) three years of

¹ JAMES MOORE, Wisconsin Department of Natural Resources, personal communication.

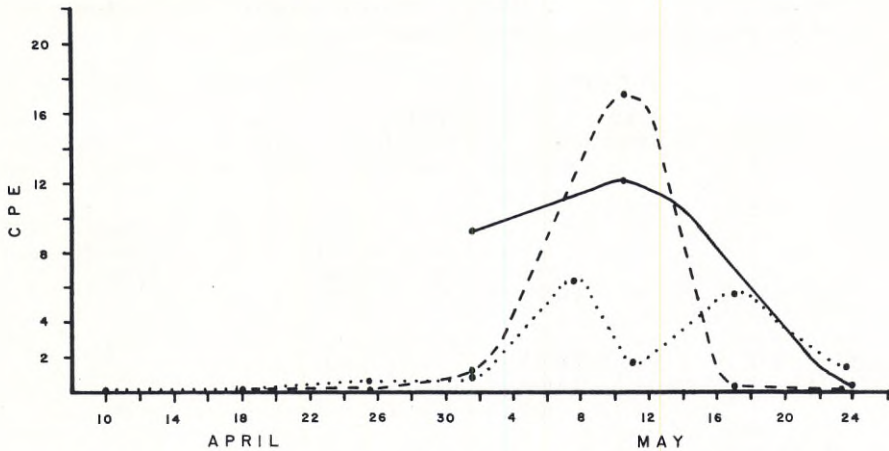


Fig. 5. Average catch per unit of effort of larval whitefish along the east side of Chambers Island (B-3) in 1968 (solid), 1969 (dashed), and 1970 (dotted) in April and May.

hatchery data show incubation times of 168, 172, and 165 days. HART (1930) found hatching started at 160 days and continued for approximately 14 days. PRICE (1940) calculated 140 to 173 days for the incubation time of whitefish at water

temperatures of 1.0 to 0.0 C, however, none survived to hatch at 0.0 C.

A consistent series of average weekly CPE values in a particular area allow one to calculate approximate larval densities. The area of North Bay 1 m

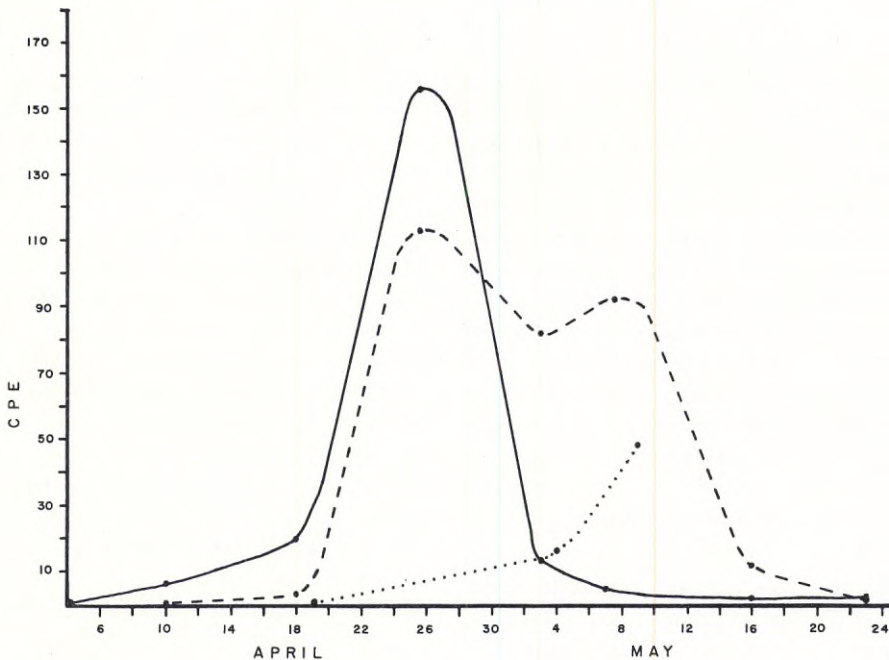


Fig. 6. Average catch per unit of effort of larval whitefish during April and May, 1970, in North Bay (dashed) at M-3 (solid), and in Europe and Newport Bay combined (dotted).

Table 6. Estimated numbers of larval whitefish in North Bay in water 0–1 m deep. Average depth of water assumed to be 0.5 m. Efficiency of sampling net assumed to be 90 percent on April 11, thereafter falling 5 percent per week.

Date	Night CPE North Bay	Total larvae (thousands)	Adjustment factor	Adjusted total larvae (thousands)	Number of larvae per cubic meter	Number of larvae per acre	Number of larvae per hectare
4/11/70	1.8	55	1.11	61	0.04	86	213
4/18/70	6.2	188	1.18	222	0.15	312	771
4/26/70	240.0	7294	1.25	9118	6.0	12,824	31,689
5/ 3/70	173.0	5258	1.33	6993	4.9	9,835	24,303
5/ 8/70	178.0	5410	1.43	7736	5.4	10,880	26,886
5/16/70	28.7	872	1.54	1343	0.93	1,889	4,668
5/24/70	4.3	131	1.67	219	0.15	303	761

or less deep is approximately 2.88 km² (713 acres). With an average depth of 0.5 m, the volume is 1,439,000 m³. Since an average unit of effort was 47.4 m³ of water strained, the average CPE times the ratio of the two volumes (30,391) provides an estimate of total larvae if the net was 100 % efficient. At best, the net was probably only 90 % efficient. SOUTHWARD (1970) found that a 1 m diameter monofilament nylon net was only 82 % efficient when towed at 4 knots. I have assumed the net lost 5 % efficiency per week during the field season.

North Bay alone supports a very large number of newly hatched whitefish in April and May. At the peak of hatching, an estimated 9.1 million larval whitefish were in the shallow water (Table 6). For the next two weeks the numbers were fairly steady at 6.9 and 7.7 million. By May 24, when the population was into the "fry" stage, 219 thousand remained. In terms of larvae per cubic meter, the highest number occurred in April 26, when 6.0/m³ were present. The next two weeks had 4.9 and 5.4/m³. On April 26 there were an estimated 12,824 larvae per acre, and on the next two weeks, 9,835 and 10,880 per acre. If the water area at a depth of 1 to 1.6 m is added to the previous calculations, 1.5 km² more surface area is available to the larvae in North Bay. Because only an occasional tow was made in water of this depth and the number of larvae few or none, no estimate was made.

The inshore area at M-3 maintained a small population of larval whitefish, that after several days moved into North Bay or some other bay.

The greatest number was on April 26, when the zone held 1.2 million larvae. On May 3 and 8 the number had dropped to 93,000 and 32,000, which represented about 1/75 and 1/250 of the North Bay population on the same dates.

The east side of Chambers Island (B-3) also functions as large holding area but not to the extent of North Bay. The total number of larvae utilizing the east side of Chambers Island was about 1 % of the North Bay population (Table 7). The highest ever recorded was on May 10, 1969, when 341,000 were estimated (assuming a strip 80 m wide by 5446 m long by 1 m deep). No other time ever exceeded 100,000 larvae at B-3. It is impossible to determine if 1969 or 1970 more nearly resembles a normal year. The number per cubic meter averaged 1/15 the North Bay population and the number per acre was much lower.

In Big Bay de Noc on May 6, 1970, an average CPE of 106.8 was obtained on a sunny calm day with 24 tows (Valentines and Kates Bay). Converting with a night factor of 2.1 and expressed as number per cubic meter, this becomes 5.62, which is very similar to the North Bay population. It is the Big Bay de Noc stock from which Chambers Island fish are thought to have originated. From this larval density the larvae probably spread to other areas.

Size and growth of larvae

The Green Bay larvae arrived at Chambers Island at similar average lengths for the three years. Average total lengths were 12.7, 12.0, and 12.4 mm on May 2, 1968, 1969, and 1970 (Table 8). In

Table 7. *Estimated numbers of larval whitefish along the east side of Chambers Island in a strip 80 m wide by 5.45 km long by 1 m deep. Water depth varies to 2 m in area but only surface 1 m considered in calculations.*

Date	Night CPE	Total larvae (thousands)	Adjustment factor	Adjusted total larvae (thousands)	Number of larvae per cubic meter	Number of larvae per acre	Number of larvae per hectare
5/ 2/69	1.9	18	1.11	20	0.05	202	746
5/10/69	31.5	289	1.18	341	0.78	3156	7799
5/16/69	0.3	3	1.25	4	0.01	41	101
4/25/70	0.4	4	1.11	4	0.01	41	101
5/ 2/70	2.1	19	1.11	21	0.05	202	499
5/ 7/70	7.3	67	1.18	79	0.18	728	1799
5/16/70	7.4	68	1.25	85	0.20	809	1999
5/23/70	1.5	14	1.33	19	0.04	162	400

1968 and 1969 the larvae had grown well by May 10 (1 and 2.1 mm respectively) but in 1970 they averaged only 0.4 mm longer by May 10. The two peaks in the CPE curve (Fig. 5) at B-3 in 1970 suggest that many newly-hatched joined the extant population between May 2 and 10, thus reducing the average total length. After May 10, the 1970 population grew well, averaging at least 1 mm per week increase in total length.

All of the April collections at M-3 were of larvae not over several days old. The first collection on April 10, 1970 averaged 13.6 mm. Thereafter the average total length did not increase above 13.9 mm until after May 4, and even then newly hatched fish continued to keep the average total lengths low. The collections on April 18 and 26 were taken at the peak of hatching and averaged 13.9 and 13.8 mm. Because these fish were from one to four days old, the best estimate of size at hatching was 13.7 ± 0.3 mm. FABER (1970) reported 13.0 mm as average hatching size and HART (1930) found 12.1 ± 0.2 mm in the Bay of Quinte, but from Lake Nipigon they were 14.3 ± 0.2 mm. Whitefish eggs reared in the laboratory by HALL (1925) at 10–11 C hatched at 13.4 to 15.0 mm and when PRICE (1940) incubated whitefish eggs at 0.5 C they hatched at 12 to 14 mm.

The North Bay larvae on all dates were larger than at M-3, (Fig. 7). As the spring progressed the relative difference in the average total lengths at the two stations became greater. This reflects of course the lower proportion of newly hatched larvae in the total population in North Bay. The rate of growth in North Bay approximated the

rate of growth at B-3 for all years. By the latter half of May, however, the North Bay larvae were growing faster than the Green Bay larvae from B-3.

Total length comparisons with a Student's t-test for the data of B-3 and M-3 showed the differences were significant at $p \leq 0.01$ on all dates. For the early dates there was virtually no overlap in the size distributions of the B-3 and M-3 larvae. For example, only 10.3 % of the larvae collected at M-3 during peak hatching were less than 13.0 mm, whereas 83.8 % arriving at B-3 on April 24 and May 2, 1970 were less than 13.0 mm. At B-3 the percentage of larvae less than 12.0 mm on April 25 and May 2 combined was 33.7 and for three collections during hatching at M-3 only one of 136 larvae, was less than 12.0 mm total length.

The mean size of capture and the lack of overlap in the ranges for the index stations B-3 and M-3 indicate the M-3 larvae stock could not have provided the larval whitefish to B-3. The assumption that only the smaller larvae from M-3 were carried to Chambers cannot be accepted because the M-3 larval population had practically no individuals of small size that were common to B-3. It would not be possible for the M-3 larvae to decrease in total length during such a trip because the yolk-sac would provide adequate nourishment and the B-3 larvae arrived with fairly large yolk-sacs.

Even if the B-3 larvae would have been of equivalent size on the same dates as the M-3 larvae, this would not provide evidence of relationship because they would have to be larger to

Table 8. Average total length of larval whitefish (in mm) from three index stations on comparable dates in 1968, 1969 and 1970, Green Bay and Lake Michigan. Number measured in parentheses.

Date	1968 B-3	1969 B-3	1970 B-3	North Bay 1970	M-3 1970
4/10	—	—	—	14.0 (28)	13.6 (36)
4/18	—	11.5 (1)	—	14.4 (50)	13.9 (50)
4/25	—	—	12.1 (36)	—	—
4/26	—	—	—	14.5 (50)	13.8 (50)
5/ 2	12.7 (42)	12.0 (40)	12.4 (45)	—	—
5/ 3	—	—	—	14.7 (100)	—
5/ 4	—	—	—	—	13.8 (50)
5/ 7	—	—	12.9 (50)	—	—
5/ 8	—	—	—	15.4 (50)	14.2 (50)
5/10	13.7 (50)	14.1 (50)	12.9 (50)	—	—
5/16	—	14.9 (3)	14.2 (100)	16.6 (70)	14.7 (50)
5/23	—	—	15.4 (42)	—	—
5/24	—	—	—	20.8 (50)	15.0 (15)

5/5/70 Fairport 15.1 (50)

5/6/70 Valentines and Kates Bay 13.4 (50)

account for the 2 to 3 week time lag from hatching to arrival at Chambers Island. Since they were smaller even with a time lag, the lack of relationship as determined by measurement data is further confirmed.

The May 6, 1970 larval collection from Northern Green Bay had an average total length re-

markably similar to the average size of larvae at Chambers Island on that date (Table 8). The Valentines and Kates Bay specimens averaged 13.4 mm and the difference between the Chambers Island fish (12.9 mm) was not significant. The Fairport sample was 15.1 mm and differed significantly at $p \leq 0.05$ from the B-3 specimens, but not

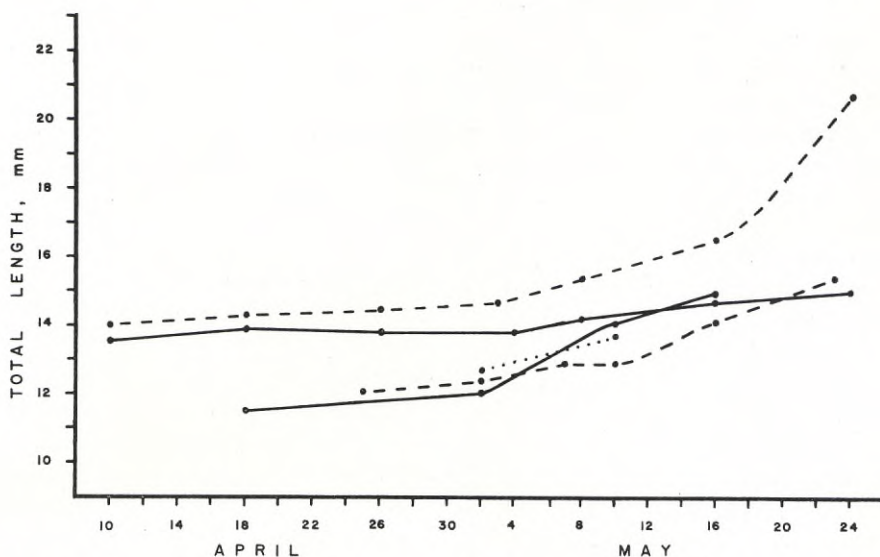


Fig. 7. Average total length of larval whitefish collected at index stations in Lake Michigan and Green Bay, all years. North Bay 1970, upper dashed; M-3

1970 upper solid; B-3 1968, dotted; B-3 1969, lower solid; B-3 1970 lower dashed.

Table 9. Length of yolk-sac of larval whitefish of Green Bay and Lake Michigan at index stations. Length measured along anterior-posterior fish axis, in millimeters. Number measured in parentheses.

Date	1968 B-3	1969 B-3	1970 B-3	North Bay 1970	M-3 1970
4/10	—	—	—	1.4 (28)	1.6 (36)
4/18	—	0.8 (1)	—	1.0 (50)	1.7 (50)
4/25	—	—	1.4 (36)	—	—
4/26	—	—	—	1.3 (50)	1.6 (50)
5/ 2	0.8 (42)	1.3 (40)	1.0 (43)	—	—
5/ 3	—	—	—	0.5 (100)	—
5/ 4	—	—	—	—	0.8 (50)
5/ 7	—	—	0.8 (50)	—	—
5/ 8	—	—	—	0.4 (50)	0.6 (50)
5/10	0.4 (50)	0.4 (50)	0.6 (50)	—	—
5/16	—	0.1 (3)	0.3 (100)	0.3 (50)	0.3 (50)
5/23	—	—	0.1 (42)	—	—
5/24	—	—	—	0.0 (50)	0.4 (15)

5/5/70 Fairport 0.4 (50)

5/6/70 Valentines and Kates Bay 0.6 (50)

from the North Bay specimens. The Fairport larvae could have come from the Valentines and Kates Bay stock and merely were more advanced or they could have come from a separate Lake Michigan stock.

The Valentines and Kates Bay larvae were approximately 1 to 3 weeks old as judged by size of yolk-sac and chromatophore development, which would place their average size at hatching between 11.5 and 12.5 mm total length. The slopes of the growth curves for the B-3 larvae (Fig. 7) indicate they hatched at a length very near 12.0 mm in all three years. These data suggest the Chambers Island population could easily have come from the Big Bay de Noc stock.

Yolk sac utilization

The larvae that arrived at Chambers Island (B-3) by May 2 had yolk-sacs that indicated they were more than seven days old in 1968 and 1970, and at least this age in 1969 (Table 9). The larger size of the yolk-sacs on equivalent dates in 1969 provides further evidence that the larval whitefish hatched later and arrived later at B-3 than in other years. The initial size of the yolk-sac for the Green Bay stock is unknown, but continuation of the slopes of Figure 8 and comparison with Lake Michigan larvae, indicate it is probably near 1.5 mm. If the average yolk-sac size for all three

years on May 1 and 2 is compared to the decrease in all yolk-sacs against time (Fig. 8), the time of peak hatching for the B-3 larvae would be April 16 to 26. The larvae arrived a B-3 at a stage comparable to FABER's (1970) second stage larvae which had formed pelvic fins. He believed his specimens were transient at his index stations when large numbers of second stage larvae arrived early, but he gave no yolk-sac information.

The utilization of the yolk-sac in all years at B-3 was similar. By May 16 the yolk reserves were almost completely exhausted. HART (1930) reported yolk-sac disappearance in the first week of May in the Bay of Quinte, but he did not make actual measurements. Rather, he referred to them as being apparent, reduced, or absent; and without the aid of a microscope, yolk-sacs 0.5 to 0.1 mm are practically undetectable. His specimens were almost identical in size on equivalent dates as the B-3 larvae.

The newly hatched larvae from Lake Michigan at M-3 had the same size yolk-sacs at equivalent dates as the B-3 larvae (Fig. 8). At first this seems somewhat surprising because the M-3 larvae were larger on comparable dates. But one should expect larger larvae to have smaller yolk-sacs only if the two groups hatched at the same size. Since the M-3 larvae hatched larger with larger yolk-sacs equiva-

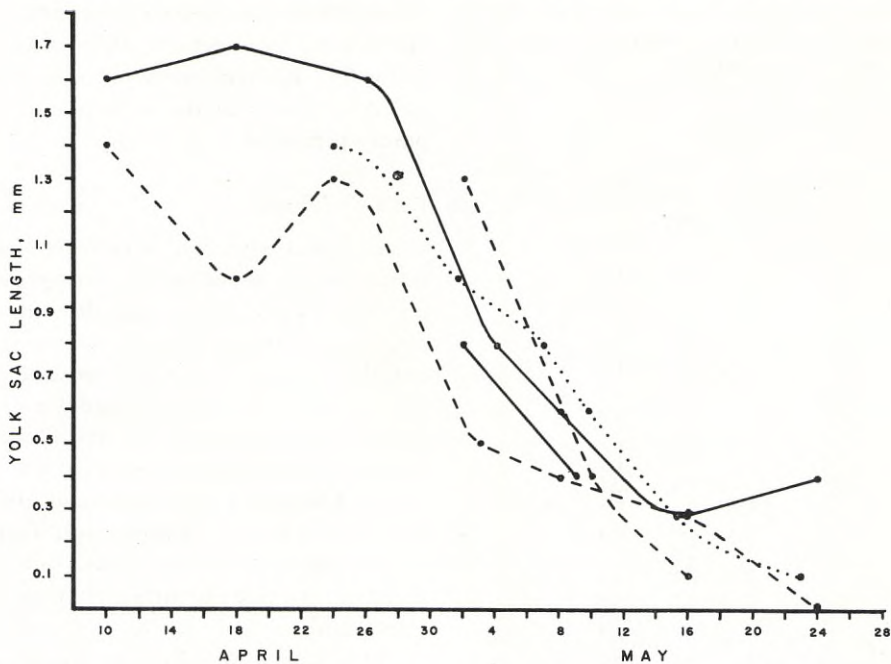


Fig. 8. Average size (length) of yolk sac of larval whitefish collected at index stations in Lake Michigan and Green Bay, all years. North Bay 1970, dashed beginning on April 10; M-3 1970, upper solid; B-3 1968, lower short solid; B-3 1969, dashed beginning on May 2; B-3 1970, dotted.

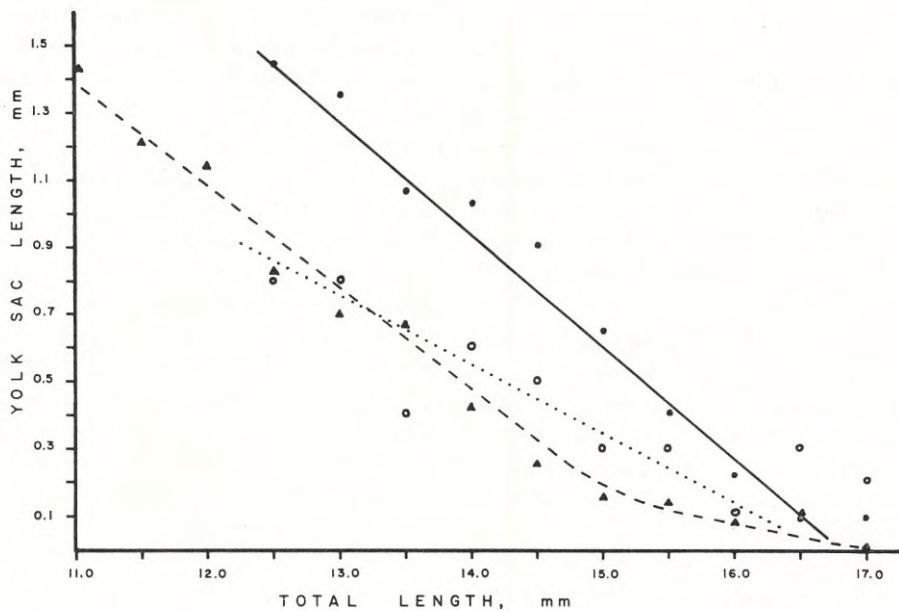


Fig. 9. Yolk-sac size averaged by total length group of larval whitefish from index stations in Lake Michigan and Green Bay. Solid line, North Bay and M-3 collections of 1970 combined; triangles and dashed line, all years of B-3 collections combined; open circles and dotted line, Big Bay de Noc 1970 specimens combined.

Table 10. Yolk-sac sizes for larvae collected in 1968—1970, grouped by one-half millimeter fish sizes and rounded to nearest tenth millimeter. Number of fish used below column. All dates of collection combined. Data from April and May.

Size of larvae ¹	1968 B-3	1969 B-3	1970 B-3	1970 North Bay	1970 M-3	Northern Green Bay
10.5	0.4 ²	0.8 ²	—	—	—	—
11.0	1.3	1.6	1.4	—	1.5 ²	—
11.5	1.0	1.5	1.2	—	—	—
12.0	1.0	1.7	1.0	—	1.4	—
12.5	0.7	0.9	0.9	0.6 ³	1.5	0.8
13.0	0.3	0.8	0.6	1.3	1.5	0.8
13.5	0.4	0.4	0.5	0.9	1.2	0.4
14.0	0.5	0.3	0.4	0.9	1.1	0.6
14.5	0.3	0.2	0.2	0.7	1.1	0.5
15.0	0.1	0.1	0.3	0.6	0.7	0.3
15.5	0.2	0.1	0.1	0.4	0.5	0.3
16.0	0.1	0	0.2	0.3	0.1	0.1
16.5	0.1	—	0.1	0.1	0.1	0.3
17.0	0	—	0	0.1	0.1	0.2
17.5	—	—	0	0.1	—	0
18.0	—	—	—	0	0	—
	90	89	321	295	297	93

¹ Size given is midpoint of class interval to which yolk-sacs were grouped and averaged.

² Only one fish at this size.

³ Only five fish at this size.

lent date comparisons are not meaningful. To compare populations the yolk-sac data were averaged by length intervals of 0.5 mm total length (Table 10). At all equivalent sizes the M-3 and North Bay had larger yolk-sacs than the Chambers Island larvae (Fig. 9). By the latter third of May, all larvae at all index stations had essentially exhausted their reserve food supply of yolk material.

Most of the Lake Michigan larvae used up their yolk-sacs 3.5 to 4.5 weeks after hatching. HART's larvae exhausted theirs after three weeks and JOHN and HASLER (1956) report complete utilization of the cisco's (*Leucichthys artedii*) yolk-sac after six days at 14 to 18 C. The several week period after hatching may provide a buffer system for the larval whitefish whereby they could cross large expanses of water lower in plankton than the warmer bays near the spawning grounds. After the middle of May, they become entirely dependent on the zooplankton for growth and maintenance.

Whatever the movement of the larvae or the environmental influences on them after later May, it appears that both stocks prior to this time had sufficient yolk material to hold them over temporary periods of food shortage.

Food of Larvae

The larval whitefish taken at B-3 had food in their stomachs at the earliest date of collection for all years (Table 11). Copepods were always the most important food organisms in terms of volume, and the average number per stomach varied from 2.1 to 26.9. The rotifer *Notholca spp* was not ignored in any year and on May 10 and 15, 1970, almost 30 per stomach were found in the B-3 larvae. Copepod nauplii were also utilized in the diet of B-3 larvae. Diatoms were found in most larvae stomachs but the number was never high. *Daphnia spp* and *Bosmina spp* were found very infrequently.

The existence of a well-developed yolk-sac did not preclude extensive feeding by the larvae. The early May specimens in all years had fairly large yolk-sacs (50 % of maximum or more) and all larvae were feeding. Only few empty stomachs were observed from the entire number of larvae examined on all dates (Tables 11 and 12). These fish usually had some sort of morphological deformity. The April 24, 1970 sample had yolk-sacs of 1.4 mm and these fish had an average of 2.1 copepods per stomach.

The North Bay and M-3 larvae had stomach contents very similar to the Green Bay larvae (Table 12). As in Green Bay, *Cyclops bicuspidatus* and *Diaptomus spp* were the predominant copepods. Other zooplankton that occurred infrequently were *Bosmina spp*, *Eucyclops agilis*, *Daphnia spp*, and *Keratella spp*. These latter organisms began to occur in the stomach after May 3 but only in limited quantities of 0.1 to 0.4 (average) per stomach. The rotifer *Notholca spp* became increasingly important as the spring progressed at both M-3 and North Bay.

The samples taken at night in North Bay did not differ significantly from the day samples taken at M-3 if the size difference of the specimens is considered. Many of the night samples were collected two to six hours after last twilight and all

Table 11. Food of larval whitefish at Station B-3 in central Green Bay expressed as average number per stomach for all larvae examined.

Date	Total length	Number of fish	<i>Cyclops bicuspidatus</i>	<i>Diaptomus spp</i>	Unidentified copepods	<i>Notholca spp</i>	Copepod Nauplii
4/24/70	12.1	36	1.8	0.1	0.2	0	2.0
5/ 1/68	12.7	42	3.1	2.2	3.4	2.6	4.7
5/ 2/69	12.0	40	1.0	0.3	1.7	0.7	1.0
5/ 2/70	12.4	45	3.9	0.1	6.6	1.7	4.5
5/11/68	13.7	50	2.3	2.0	3.0	5.1	20.4
5/10/69	14.1	50	4.0	3.9	5.7	22.1	0
5/10/70	12.9	50	0.1	0.1	2.4	29.9	2.1
5/15/70	14.1	50	6.2	0.2	20.5	28.9	0.5
5/23/70	15.4	42	8.1	0.1	12.5	19.1	0.4

were feeding actively as shown by the state of digestion.

FORBES (1883) and HART (1930) found copepods to be the most important food item for whitefish larvae. HART's specimens consumed fair quantities of *Daphnia spp* whereas FORBES' experiments

showed that *Daphnia spp* were too large for month-old larvae. This study cannot be accurately compared with either HART's or FORBES' because Hart used only 40 specimens from throughout the spring and FORBES used larvae held in aquaria. BAJKOV (1930) determined that *Bosmina spp* and

Table 12. Food of larval whitefish at station M-3 and North Bay Lake Michigan, in 1970, as average number per stomach for entire group examined

Date	Total length	Number of fish	<i>Cyclops bicuspidatus</i>	<i>Diaptomus spp</i>	Unidentified Copepods	<i>Notholca spp</i>	Dipteran larvae	Station & Day or night
4/10	13.6	36	0.1	0.2	0	0	0	M-3, D
4/10	14.0	28	0.1	0.8	0.3	0	0	NB, N
4/18	13.9	50	0.1	0	0.2	0.1	0	M-3, D
4/18	14.3	16	1.1	1.3	1.0	3.4	0	NB, N
4/26	13.8	50	0.2	0.1	0.3	0.5	0	M-3, D
4/26	14.5	50	0.6	0.2	1.3	8.2	0	NB, N
5/ 4	13.8	50	2.2	0.3	2.6	31.7	0.8	M-3, D
5/ 3	14.5	50	4.0	1.2	4.1	16.5	0.3	NB, D
5/ 3	14.9	50	3.4	2.1	6.0	14.8	0.4	NB, N
5/ 8	14.2	50	2.8	0.2	3.9	12.3	0.5	M-3, D
5/ 8	15.4	50	1.8	0.3	5.6	17.2	0.5	NB, N
5/16	15.0	50	7.8	0.4	8.7	73.4	0.3	M-3, D
5/16	16.6	50	3.5	0.1	7.6	56.6	0.1	NB, N
5/24	15.0	15	2.5	0	4.9	39.2	0.1	M-3, D
5/24	20.8	50	25.4	0.2	17.2	68.6	7.1	NB, N
5/ 5	15.1	50	3.3	2.8	5.8	40.5	2.6	Fairport, N
5/ 6	13.4	50	2.8	0.1	4.2	1.9	0.1	Valentines D

Chironomus spp larvae were most important to the 17 fry (no yolk-sac fish examined) which he examined in Manitoba. Copepods were third in importance. The average length of his specimens was 19.1 mm and they would be expected to eat more of the larger organisms. LINDSTRÖM (1962) found *Bosmina* most important in the diet of three species of whitefish during their first summer in Sweden.

A plot of average larval length against total number of copepods in the stomachs yielded a straight line for the Green Bay and Lake Michigan larvae. Since the yolk-sac disappeared within the range of average lengths plotted, this suggests no sudden shift to a completely external food source. The so-called "critical period" involving an abrupt transition from yolk feeding to zooplankton does not seem to be important to lake whitefish larvae. They were feeding long before the yolk-sac was exhausted and there was no noticeable increase in consumption of zooplankton at the sizes of yolk-sac disappearance. JOHN and HASLER (1956) showed that lake herring larvae began feeding within one day after hatching and FORBES (1883) concluded that lake whitefish feed before full utilization of the yolk-sac. BRAUM (1967) found that the time of first feeding for the whitefish (*C. wartmanni*) of Lake Constance depends primarily on the water temperature; ranging from 5 days to 18 days for fish held at 14 to 5 C. He also found active feeding well before the disappearance of the yolk-sac.

Interactions With Other Fish

Although no determined effort was made to gather data on fishes associated with the larval whitefish in early spring, observations made over the course of three years and related research on the entire fish complex of Green Bay enable some comments to be made concerning the relative influence of the major fishes on the larval whitefish.

The lake whitefish of Green Bay and adjacent Lake Michigan seem to have benefited by the striking changes in the species composition of these waters over the past two decades. Commercial catches of whitefish have risen steadily in Green Bay and Northern Lake Michigan since 1960 and now they are as abundant as before the extreme lows of the late 1950's. For example the October

catch of whitefish adjacent to North Bay in 1967—71 was 12, 18, 49, 104, and 201 thousand pounds. In general the data of HOAGMAN (1970) and WALTER and HOAGMAN (1971) show the lake herring is practically extinct, the sea lamprey (*Petromyzon marinus*), under fair control, the smelt (*Osmerus mordax*) at tremendous abundance, the alewife (*Alosa pseudoharengus*) is the most abundant pelagic fish in summer, the yellow perch (*Perca flavescens*) at very low abundance, the walleye (*Stizostedion vitreum*) at very low abundance, and the lake trout (*Salvelinus namaycush*) low. The round whitefish (*Prosopium cylindraceum*) is still present, but its abundance is low and it never was very abundant in these waters. The species that *could* have the greatest effect on the newly hatched whitefish are the perch, smelt and alewife. For example, HART (1930) found 3500 whitefish larvae in the stomachs of 15 perch.

In the areas investigated by this study, by the time larval whitefish make their way to shallow water the smelt have vacated these areas. Adult smelt were captured April 12 through 25 along the east side of Chambers Island in 1969 and 1970. This was approximately two weeks before the newly hatched whitefish arrived in any numbers. By May 1 around Chambers Island smelt were absent in the shallow water (0.5—1.5 m) where larval whitefish were captured. In the 1970 smelt were never noticed in North Bay or at M-3 even though early April observations were made. On May 5 and 6, 1970, no smelt were observed at several locations in Big Bay de Noc while larval whitefish were being captured. According to local commercial fishermen, the smelt have left the streams and shallow shore areas by mid-April.

The yellow perch was at an all time high in abundance from 1954—66. The whitefish adult stocks during this time fell to near extinction and then rose in 1962—66 to one of its highest levels. Such a phenomenal return of the whitefish indicates clearly the larvae and young were not influenced significantly by the high population of perch in these years. The perch in Green Bay and adjacent Lake Michigan have probably been reduced in abundance by the alewife (SMITH, 1970). It seems adult perch have been displaced offshore and the alewife competes with and may even consume the larvae of the perch inshore.

The competition by other species of larvae on larval whitefish was negligible or non-existent. In mid-April burbot larvae (*Lota lota*) were often taken in the tow nets with larval whitefish near Chambers Island but never in large quantities. By May the burbot larvae disappeared. No burbot larvae were ever captured at M-3 or in North Bay and no other larvae of any species were ever taken at any station in any year. The reason cannot be the mesh size of the nets because burbot larvae are very small (3—5 mm) and these were readily captured.

The most recent arrival to upset the entire fishery balance in Lake Michigan and Green Bay has been the alewife. Its effect on other fishes has been postulated by many but only SMITH (1968a, 1968b, 1970) defines and details its influence with any degree of completeness. The alewife's potential for devouring larval fishes can be inferred from its preference for large plankton (BROOKS and DODSON 1965; WELLS 1970). SMITH (1970) reports on a school of alewives consuming larval smelt, and I have fed alewives larval whitefish in the laboratory but they will also take many species of larvae (HOAGMAN, 1974).

Along the east shore of Chambers Island, the first dead alewives appear after mid-May. The main alewife population does not arrive until June in central Green Bay (REIGLE, 1969; HOAGMAN, unpublished data). In 1970 the first alewives were noticed around M-3 on May 16 as scattered dead individuals. By May 24 the population must have increased because dead alewives were much more common. On both dates no living alewives were observed in North Bay and limited shore seining at night yielded only common shiners (*Notropis cornutus*). The stomachs of the shiners did not contain larval whitefish. Moonlight Bay, which is the first bay south of North Bay, had a large school of alewives in it on the night of May 16, 1970. These fish were found in 1 to 2 m of water and were actively dashing around at the surface. Larval whitefish were also collected in Moonlight Bay that night but they were only found in water 0.3 to 1 m deep and no alewives were observed there. By June 6 the major alewife population had moved to the shallow water in North Bay and Green Bay but by this time the young whitefish had left for deeper water.

The effect of the alewives on the whitefish population can only be speculated. If they have any effect on the larval whitefish, it probably would be when the habitats of the two overlap and the young whitefish are small enough for the alewife to eat, which is less than 17 mm (HOAGMAN, 1974). These events seem rather mutually exclusive in Green Bay and adjacent Lake Michigan. If the alewives do arrive early enough to crop a segment of the larval whitefish population, they probably would eat only the smallest individuals because the average size of the larvae is then close to 20 mm total length.

The present Green Bay and northern Lake Michigan whitefish stock is very abundant now and has been since 1962 (WALTER and HOAGMAN, 1971) and it has become the fastest growing and earliest maturing stock of any reported in the Great Lakes (PIEHLER, 1967; BROWN, 1968; DE MUTH, 1970). During the same time period, since 1962, the alewife population had risen to a very high abundance and apparently reached its peak in 1967. If the alewife stocks were in any significant way cropping larval whitefish, successful recruitment of whitefish would not have taken place to nearly the same degree. The adult whitefish stock since 1962 has been as abundant as any period since 1929 and in several years more abundant. It is possible that the alewife may actually be contributing in some way to the success of whitefish year classes by controlling the abundance of species which previously had a negative effect on whitefish.

In South Bay, Lake Huron, when the young whitefish leave the inshore water they inhabit the bottom where the thermocline obliquely crosses (RECKAHN, 1970). If they do the same in Green Bay and adjacent Lake Michigan, they would be in an area inhabited mainly by smaller fishes (troutperch, sticklebacks, younger smelt, and some cottids). Here competition would be present but predation on juvenile whitefish would probably be low.

IV. REFERENCES

- БАЖКОВ, А. 1930. A study of the whitefish (*Coregonus clupeaformis*) in Manitoban Lakes. *Contrib. Canadian Biol. Fish. N.S.* 5(4): 433—455.

- BRAUM, E. 1967. The survival of fish larvae in reference to their feeding behavior and the food supply. p. 113—131. In *The Biol. Basis of Fish Prod.*, Ed.: S. D. GERKING. John Wiley and Sons. Oxford and Edinburgh.
- BROOKS, J. L. and S. T. DODSON. 1965. Predation, body size, and composition of plankton. *Science*. 150: 28—35.
- BROWN, R. J. 1968. Population structure and growth characteristics of the white fish in northern Lake Michigan 1929—67. MS Thesis, Sch. Nat. Res., Univ. Michigan. 61 p.
- CASANADY, G. T. 1964. Hydrodynamic studies on Lake Huron at Baie du Dore, summer 1964. *Gr. Lakes Inst. Rep.* PR 19. Univ. Toronto, Ont. Canada. 145 p.
- CHRISTIE, W. J. 1963. Effects of artificial propagation and the weather on recruitment in the Lake Ontario whitefish fishery. *J. Fish. Res. Bd. Canada*, 20(3): 597—646.
- DOAN, K. H. 1942. Some meteorological and limnological conditions as factors in the abundance of certain fishes in Lake Erie. *Ecol. Monogr.* 12(3): 293—314.
- DEMUTH, P. R. 1970. A study of the growth characteristics of the whitefish population of Green Bay. *Summer Sci. J.* 2(1): 1—23.
- FABER, D. J. 1970. Ecological observations on newly hatched lake whitefish in South Bay, Lake Huron. p. 481—500. In *Biology of Coregonid Fishes*, Eds.: C. C. LINDSEY and C. S. WOODS. Univ. Manitoba Press, Winnipeg, Manitoba.
- FORBES, S. A. 1883. The first food of the common whitefish. *Illinois Nat. Hist. Sur. Bull.* 1(6): 87—99.
- HALL, A. 1925. Effects of oxygen and carbon dioxide on the development of the whitefish. *Ecology* 6: 104—116.
- HART, J. L. 1930. The spawning and early life history of the whitefish, *Coregonus clupeaformis* (MITCHILL), in the Bay of Quinte, Ontario. *Contrib. Canadian Biol. Fish.* 6(7): 167—214.
- HOAGMAN, W. J. 1970. Fluctuations in the populations of lake herring (*Leucichthys artedii*) and rainbow smelt (*Osmerus mordax*) in Northern Green Bay, 1929—1970. *Proc. Lake Superior Biol. Conf. Wisconsin State Univ., Superior Wisc.* (In Press).
- 1973. Vital activity parameters as related to the early life history of larvae and post-larvae lake whitefish (*Coregonus clupeaformis*). *Proc. Internat. Sym. Early Life History of Fish.* Oban, Scotland, May 1973. 12 p.
- 1974. The feeding of larval lake whitefish (*Coregonus clupeaformis*) to alewives (*Alosa pseudoharengus*) in the laboratory. *J. Fish. Res. Bd. Canada*. (In Press).
- JOHN, D. R. and A. D. HASLER. 1956. Observations on some factors affecting the hatching of eggs and the survival of young shallow-water cisco. *Leucichthys artedii* LE SUEUR, in Lake Mendota, Wisconsin. *Limnol. Oceanogr.* 1(3): 176—193.
- LAWLER, G. H. 1965. Fluctuations in the success of year-classes of whitefish populations with special reference to Lake Erie. *J. Fish. Res. Bd. Canada*, 22(5): 1197—1227.
- LINDSTRÖM, T. 1962. Life history of whitefish young (*Coregonus*) in two lake reservoirs. *Rep. Inst. Freshw. Res., Drottningholm.* 44: 113—144.
- 1967. On the importance of growth and spawning site ecology of whitefish (*Coregonus*) for survival of the young. *Rep. Inst. Freshw. Res. Drottningholm.* 47: 128—146.
- NOBLE, R. L. 1970. Evaluation of the Miller high-speed sampler for sampling yellow perch and walleye fry. *J. Fish. Res. Bd. Canada*, 27(6): 1033—1044.
- PIEHLER, G. R. 1967. Age and growth of the common whitefish, *Coregonus clupeaformis* (MITCHILL), of northern Lake Michigan and Bay de Noc areas. MS Thesis, Mich. State Univ., Dept. Fish. Wildl. Lansing, Mich. 94 p.
- PRICE, J. W. 1940. Time-temperature relations in the incubation of the whitefish, *Coregonus clupeaformis* (MITCHILL). *J. gen. Physiol.* 23: 449—468.
- RECKAHN, J. A. 1970. Ecology of young lake whitefish (*Coregonus clupeaformis*) in South Bay, Manitoulin Island, Lake Huron. P. 437—460. In *Biology of Coregonid Fishes*, Eds.: C. C. LINDSEY and C. S. WOODS. Univ. Manitoba Press, Winnipeg, Manitoba.
- REIGLE, N. J. 1969. Bottom trawl explorations in Green Bay of Lake Michigan, 1963—65. *Fish Wildl. Ser. Bur. Comm. Fish. Circ.* 297. 14 p.
- SMITH, S. H. 1968a. The alewife. *LIMNOS* 1(2). 9 p.
- 1968b. Species succession and fishery exploitation in the Great Lakes. *J. Fish. Res. Bd. Canada*. 25(4): 667—693.
- 1970. Species interactions of the alewife in the Great Lakes. *Trans. Amer. Fish. Soc.* 99(4): 754—765.
- SOUTHWARD, A. J. 1970. Improved methods of sampling post-larval young fish and microplankton. *J. Mar. Biol. Assoc., U.K.* 50: 689—712.
- WALTER, G. and W. J. HOAGMAN. 1971. Mathematical Models for Estimating Changes in Fish Populations with Applications to Green Bay. *Proc. 14th Conf. Great Lakes Res.* 170—184. *Int. Assoc. Great Lakes Res.* 170—184.
- WELLS, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. *Limnol. & Oceanogr.* 14(4): 556—565.

Preferences Among Juvenile Char (*Salvelinus alpinus* L.) to Intraspecific Odours and Water Currents Studied with the Fluvium Technique

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I. INTRODUCTION

The aim of the present study was to determine the role of olfaction in intraspecific preferences or schooling behaviour among juvenile char. Findings of many investigators (TODD *et al.*, 1967; HEMMINGS, 1966; SHAW, 1962; BARDACH and TODD, 1970; KLEEREKOPER, 1969, 1971; and others) have indicated that olfaction and vision have specific roles of importance for communication between fish. Methods for showing such effects quantitatively are rare. Olfactory responses can be studied directly and easily quantified, however, by means of the fluvium technique (HÖGLUND, 1961), which was somewhat modified for the present study (see Figs. 1 and 2). The effect of visual stimuli can also be studied indirectly by comparing results arrived at with fluvium tests performed in light and darkness.

According to TODD *et al.* (1967) the main source of olfactory stimuli involved in intraspecific recognition among fishes is the external mucus layer. From this, chemical substances are excreted into the surrounding water. The problem was now to produce a choice situation between odorous and odour-free water so that the preferences could easily be quantified. First the normal behaviour of juvenile char concerning water currents was examined by the following experiments. A study was made of free-swimming *versus* resting on the bottom at various flow velocities and the rheotactic responses were recorded (Experiment I in Fig. 2). Preferences for stagnant water or water currents at various flow rates were also investigated (Experiment II in Fig. 2).

Finally, the preferences were recorded when the young char were given a choice between one

odorous water current and one free from odour. This test was performed in an illuminated confined space (the test yard) of the experimental flume (Experiment III in Fig. 2).

The latter type of test was also performed with fishes whose olfactory organs had been extirpated. It is planned to repeat these tests in future experiments with intact fishes in infrared light beyond the region of the spectrum visible to fish.

II. MATERIAL AND METHODS

A. Fish material

First-summer char (*Salvelinus alpinus* (L.)) with a mean body weight of 12.1 g (range 8.6–15.7 g) and a mean length of 11.4 cm (range 10.6–12.5 cm) were used in the experiments. The fish derived from a population in Lake Hornavan, Swedish Lapland. They were hatched and reared by the breeding plant of the Fishery Board at Älvkarleby. They were kept in our laboratory in a storage aquarium with aerated water with continuous round-flow. The fish were fed daily with EWOS pellets, standard fodder size 1.

B. Water quality

The water supply both to the storage aquarium and to the fluvium is Uppsala tap water, a subsoil water deriving from an esker in the area. The chemical composition of this water, with a high ion content, is fairly constant. The main constituents are Ca^{2+} , Mg^{2+} and HCO_3^- (see HÖGLUND 1961, Table 3, p. 33, and MARCSTRÖM 1967, Table 7, p. 457). All water was aerated and the oxygen content was checked regularly by modified Winkler titration during the experimental period.

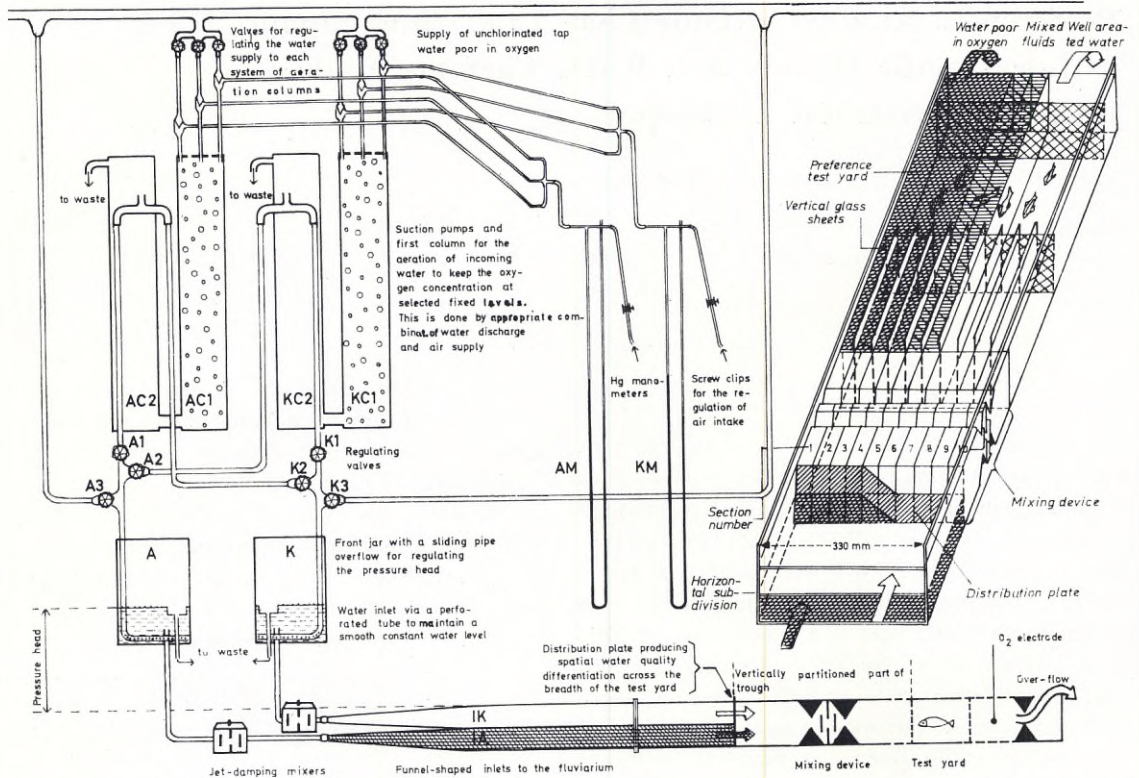


Fig. 1. General scheme of the fluvium when used in a study of the preferences of fish to spatial differentiations of dissolved oxygen in Uppsala tap water (cf. HÖGLUND, 1961). In the present study the distribution

plate was replaced by screens which were designed to produce the areal distribution of currents shown in Fig. 2, experiments II and III.

The total alkalinity and pH were also checked regularly, the former by the method of Berger (cf. KARLGRÉN, 1962) and the latter with a Radiometer PHM-26 (Table 1).

C. Test techniques.

The fluvium technique was modified for the different experiments (see Figs. 1 and 2). Three types of areal distributions in the confined space of the test yard of stagnant water and water current with and without fish odour, designated Experiment I, II, and III in Fig. 2, were established. In all experiments the momentary positions of the test fishes were recorded every 30 seconds with a 16 mm film camera (Bolex Paillard).

1. Experiment I.

No modification of the original method (HÖGLUND, 1961) was made here *i.e.* as far as possible

there was an equal flow rate over the whole width of the test yard (Fig. 1, with the distribution plate removed). The behaviour of the fishes was recorded at various flow velocities — both for ascending and descending series.

2. Experiment II.

A water flow was distributed to three of the 10 sections of the test yard. The distribution plate in Fig. 1 was replaced by a plastic plate constructed for this purpose. The latter allows alternation of the flow from one side to the other, designated here side A and side K (Fig. 2). A study of possible preferences to increasing flow rates was made.

3. Experiment III.

Two equal currents, one on each side of the test yard, were obtained as shown in Fig. 2. They passed through three sections each, leaving a space

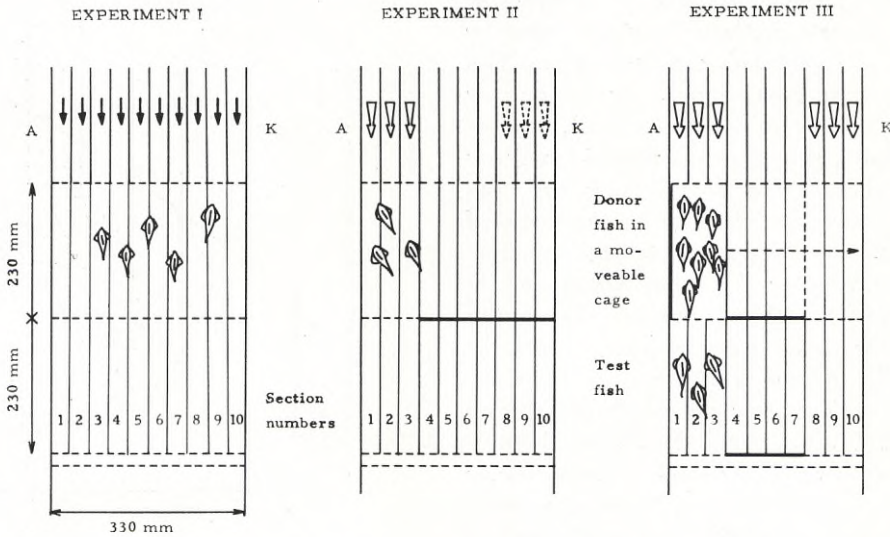


Fig. 2. The designs of experiments I—III. I. As far as possible the fish encounter an even laminar flow all over the breadth of the test yard. The degree of free-swimming and rheotactic response were studied at different flow velocities (see Fig. 3). II. The fish are given a choice between static water and flowing water in three out of ten parts of the yard alternating from one side to the other, A and K (cf. Figs. 4 and 5). III. Test fishes are allowed to swim freely about in

a yard with two identical streams separated by a zone with stagnant water in the middle of the trough. One of the streams passes a group of "donor fish". The stream thus assumed to contain fish odour alternated from one side to the other during consecutive test periods lasting for 90 min. The results arrived at with intact test fish are given in Figs. 6a, b and 7a, b. The reactions of fish whose olfactory organs had been removed are presented in Figs. 6c, d and 7c, d.

Table 1. Chemical and physical properties of the aerated Uppsala tap water used during the experimental period, based on several determinations.

Oxygen content mg/l	Alkalinity expressed as HCO_3^- mmol/l	pH	Temperature $^{\circ}\text{C}$
8.5—10.8	4.45—4.72	7.4—7.8	7.4—9.0

of relatively stagnant water in the remaining four middle sections. Furthermore, the test yard was divided lengthwise into two compartments (Fig. 2). In the up-stream compartment a moveable cage was placed. This was constructed so that water could pass through and so that it could be placed in one of the two currents in the test yard. During consecutive test periods lasting for 90 minutes each it was moved alternately from one to the other of the two currents. Seven to eight donor fishes, which were to excrete odorous substances into the water, were kept in this cage. In the down-stream compartment three or two test fishes were al-

lowed to swim about freely. They were thus given a choice between odorous and non-odorous water. Experiments both with intact fishes and with fishes whose olfactory organs had been extirpated were performed. By comparing the results from the two types of tests the consequences of olfactory stimulation for intraspecific communication could be estimated.

D. Quantitative evaluation and presentation

The number of momentary visits in each section as recorded on each frame of the film is multi-

plied by the corresponding section number. The total sum of these products from ten frames is divided by the total number of observations. This represents a mean position value for five minutes ($mpv_{5 \text{ min}}$ according to HÖGLUND, 1961, p. 46—48). The $mpv_{5 \text{ min}}$ values are plotted in diagrams as seen in Figs 4 and 6 and show the mean preferences among the fishes during the course of different parts of the experiments. By definition a mean position value of 5.5 thus indicates an indifferent reaction. The difference between this value and the actual mean position value for a certain period of time gives a reaction value, rv , with an index indicating the length of a period with identical experimental conditions. Positive values indicate *attraction* and negative values *avoidance*, in accordance with the definitions suggested by HÖGLUND (1961, p. 48—49). See also Figs 4—7.

III. RESULTS

A. Normal reactions to even water current at laminar flow rates

The percentage of free-swimming and positive rheotactic behaviour is plotted against flow velocity in Fig 3. Each dot represents a mean value from 480 observations of momentary positions at each flow rate.

An increase of about 10 % in the determined variables on increase of the flow rate from 0.4—1.2 cm/sec was found. For practical reasons the behaviour at faster flow rates could not be examined with this distribution of water flow.

B. Reactions when given a choice between stagnant and flowing water

In Fig. 4 the preferences to water current as against stagnant water are shown by plotting $mpv_{5 \text{ min}}$ values (in section breadths) against time. A comparison of the reactions at low flow rates with those at moderate rates revealed increased attraction to the current in the latter cases. When the flow rate was increased further beyond a certain level this attraction diminished again. This is shown in Fig. 5 where the degree of

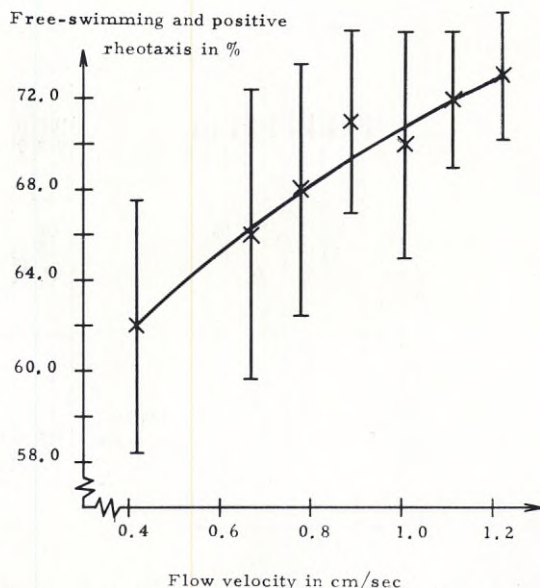


Fig. 3. Percentages of free-swimming juvenile *Salvelinus alpinus* (L.) in experiment I of Fig. 2 recorded as directed against the current at various flow rates. The vertical bars represent the standard deviation of the mean based on 120 observations in each of four experiments ($n=4$).

attraction ($rv_{30 \text{ min}}$ values) to the flowing side is plotted against the flow velocities used in this part of the study. The results presented in Figs. 4 and 5 refer to two different experimental series.

C. Preferences for intraspecific olfactory stimuli

The preferences arrived at with intact fish given a choice between odorous and non-odorous water currents are shown in Figs 6a, b and 7a, b and those for fish with their olfactory organs removed in Figs 6c, d and 7c, d. In Fig 6 $mpv_{5 \text{ min}}$ values (expressed in section breadths as unit) are given during the course of the experiments. An obvious difference is observed, as intact specimens showed a very strong preference (attraction) for the current with odorous water while the fish with their olfactory organs removed did not. Both groups, however, preferred to stay in the current rather than in the parts of the test yard filled with stagnant water.

The attraction among intact fish to the parts assumed to contain specific fish odour showed

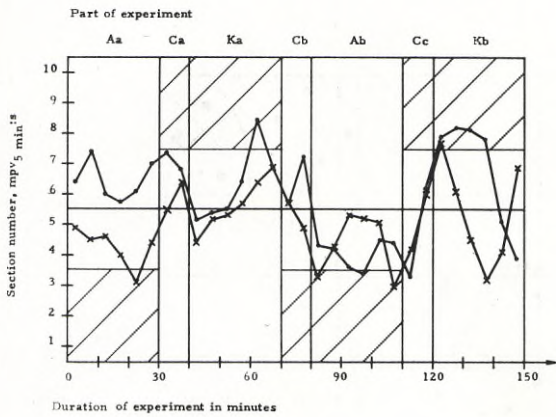


Fig. 4a.

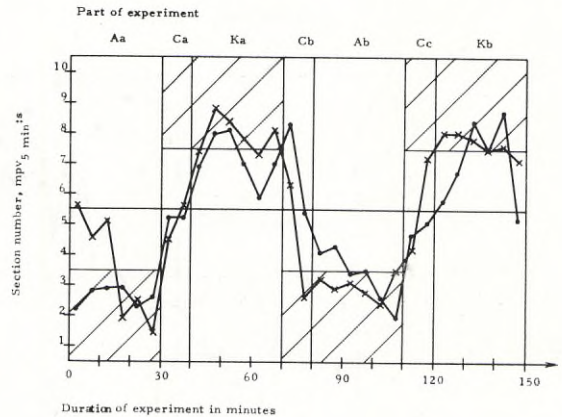


Fig. 4b.

Fig. 4. Tests performed according to experimental design II in Fig. 2. Preferences among juvenile char (*Salvelinus alpinus* (L.)) are expressed as mean position values for consecutive 5 min periods for water current or stagnant water. a. · represents the reactions when the flow rates were 0.4 cm/sec; × 1.5 cm/sec. b. · represents the rate of 2.4 cm/sec and × 3.1 cm/sec. Three test fishes were used in each experiment. The cross-

hatched area corresponds to the parts of the test yard with flowing water, and the remaining area static water. Aa, Ab and Ka, Kb represent test periods lasting for 30 minutes each with the current along either side of the trough, Ca, Cb etc. are periods when a new environment was established. Records from test periods only are presented in Figs. 4, 5, 6, and 7.

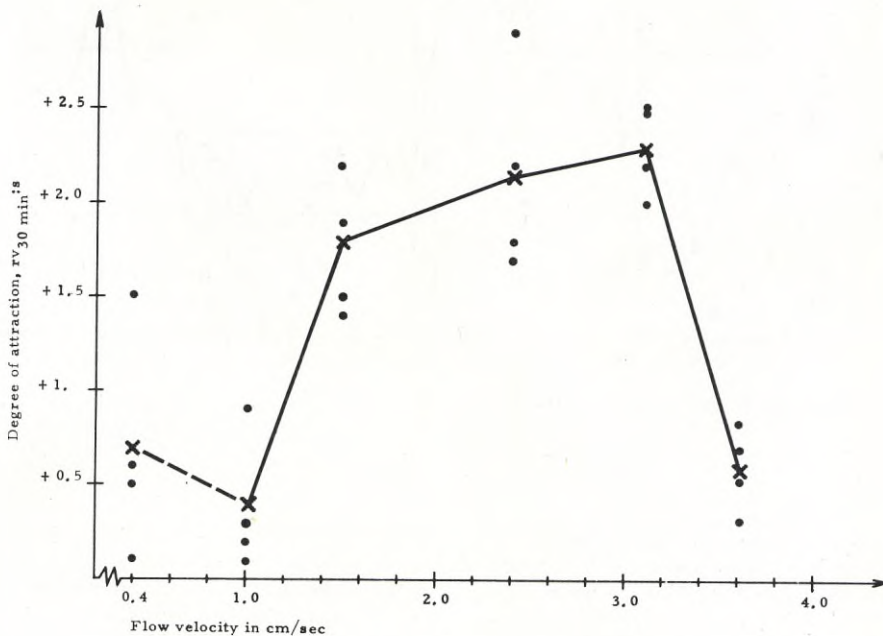


Fig. 5. The preferences (attraction) among 5 juvenile char to flowing water under various flow conditions

as in experiment II of Fig. 2 expressed as $rv_{30 \text{ min}}$ values (for definition see p. 24).

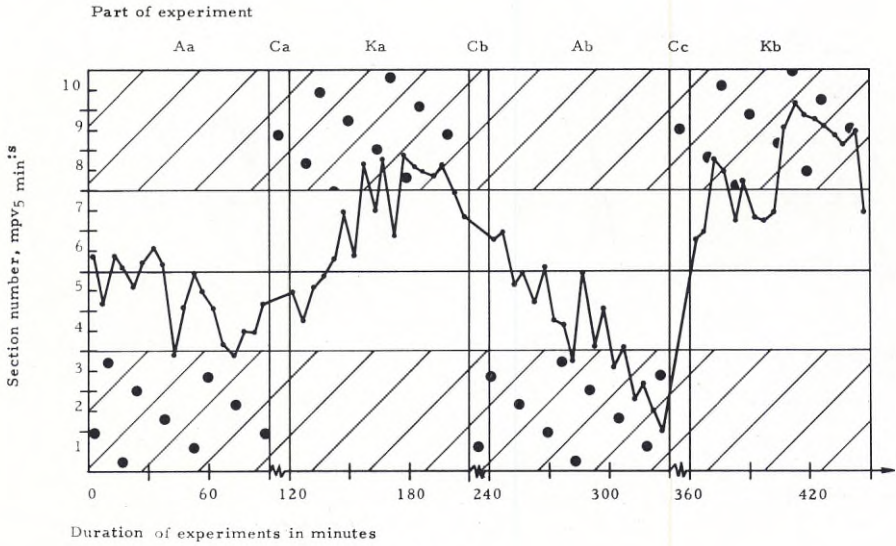


Fig. 6a.

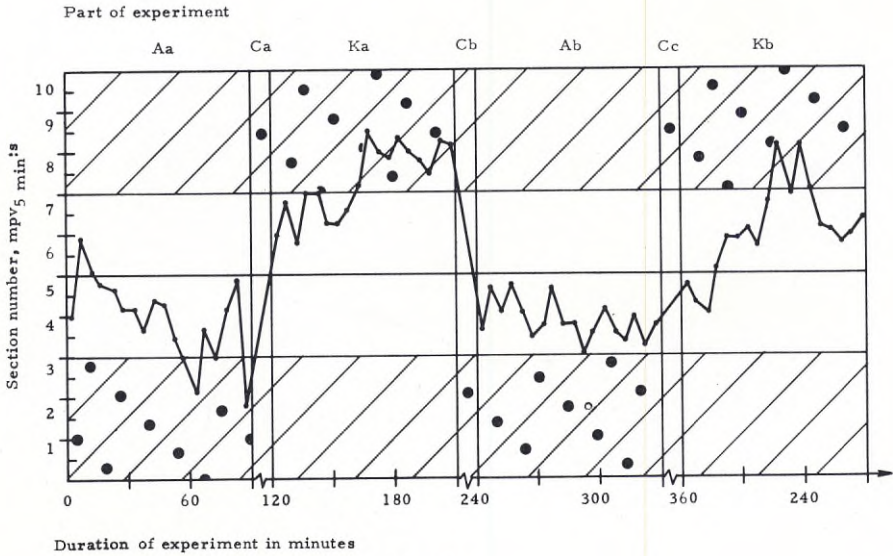


Fig. 6b.

Fig. 6. Preferences among young char (*S. alpinus* (L.)) for intraspecific odour. Three specimens were given a choice between two areas with flowing water (cross-hatched in the graphs) along each side wall and stagnant water in the middle during 90-min test periods. One flow, indicated by dots in the graphs is assumed to contain odour from 7–8 “donor fish” in the up-

stream part of the test yard. The “donor fish” could not be seen by the test fish allowed to swim freely about in the same test yard, the two parts being separated by a fine-meshed net of stainless steel. a and b refer to intact fish, c and d to fish with their olfactory organs removed. Tests as in experiment III of Fig. 2, the flow velocity in each stream was 2.0 cm/sec.

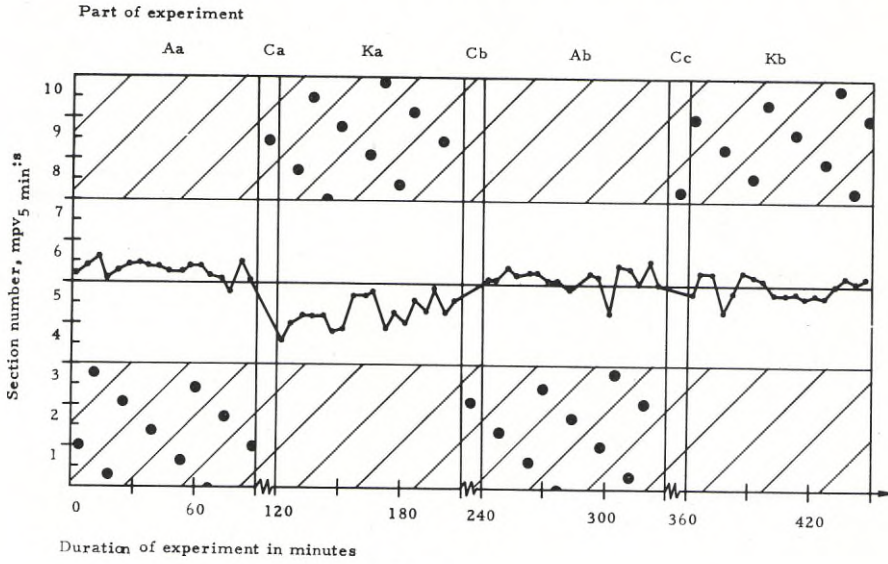


Fig. 6c.

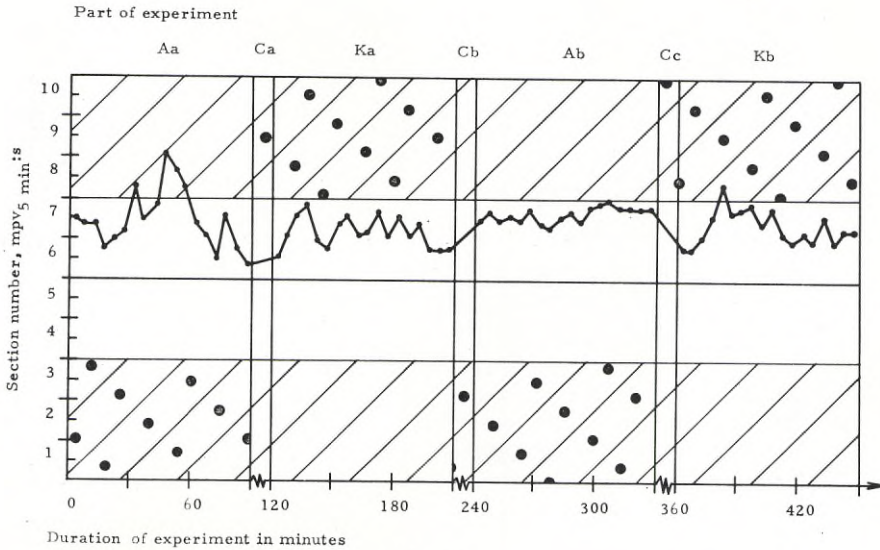


Fig. 6d.

gradually increased values during the course of an experimental period with the same areal distribution of stagnant and flowing water, the latter with and without odour (Fig. 7). It also appears from Fig. 7 that fish without olfactory organs exhibited an almost indifferent reaction with re-

gard to one or the other stream, and in several experiments even a negative reaction or avoidance of the stream passing through the cage with "donor" fish was recorded (Fig. 6c, parts Aa and Ka, and Fig. 7c).

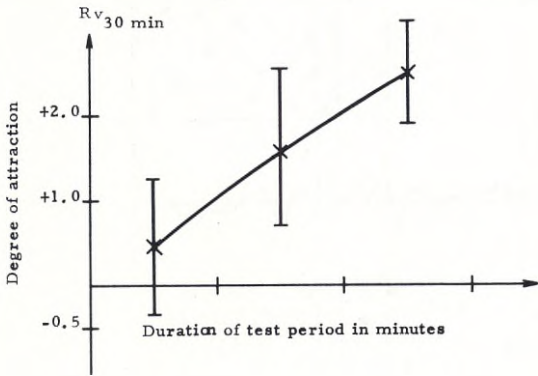


Fig. 7a

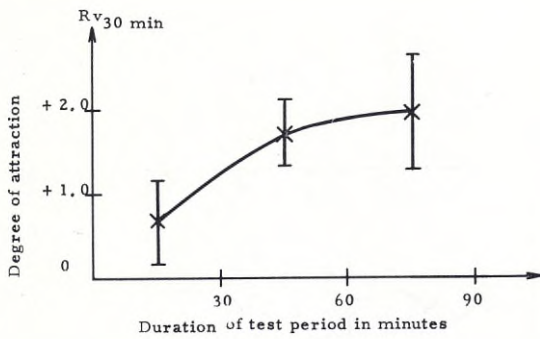


Fig. 7b

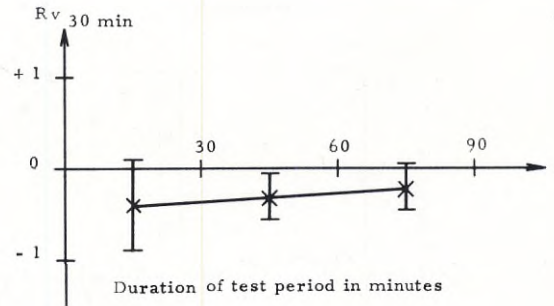


Fig. 7c

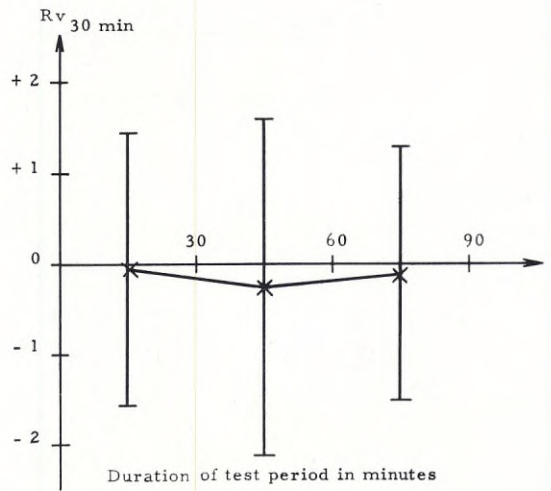


Fig. 7d

Fig. 7. The preferences among young char (*S. alpinus* (L.)) for intraspecific odour expressed as reaction values ($r_{v30 \text{ min}}$ values, for definition see p. 24) for consecutive 30-minute periods within each test period lasting for 90 min altogether. The graphs in a and b represent

the reactions of intact fishes, and those in c and d the reactions of fishes whose olfactory organs had been removed. The vertical bars represent standard deviation of the mean ($n=4$).

IV. DISCUSSION

A. Reactions of juvenile char to water currents

The aim of these studies of reactions to different water flows was to find an accurate test technique for investigating the role of olfaction in the communication between individual fish. Therefore, as these tests led to the attainment of suitable flow conditions for the identification of intraspecific attraction by odour, no further comments are

made about this part. The results are presented mainly for complete understanding for the method employed.

B. Reactions induced by presumed olfactory perception

The large difference in the standard deviations, seen in the graphs of Fig. 7, is due to the fact that in one test (Fig. 7d) the fish whose olfactory organs had been removed remained most of the

time in one current, while in another experiment (Fig. 7c) they swam from one stream to the other. In both cases, however, the fish operated on spent most of their time in the areas with flowing water. The comparatively small standard deviation values in the tests performed with intact fish are accordingly due to the more distinct preferences of these specimens for the stream containing fish odours (Fig. 7a, b).

TODD *et al.* (1967) conclude from their work on the yellow bullhead (*Ictalurus natalis*) that fish of this species recognize individuals of the same species by means of pheromones, *viz.* intraspecific chemical stimuli. MARLER and HAMILTON (1966) consider from their studies that chemical communication may play a more important role in fish behaviour than has been previously believed. One question of interest, assuming the importance of chemical stimulation is how interaction between vision, tactile stimulation and olfaction takes place. Under what conditions does one or the other play a dominant role? It seems too early to answer this question. Further supplementary experiments with the present technique may contribute to a better understanding of these problems.

According to HEMMINGS (1966) the attraction modalities involved are vision in daylight and olfaction in darkness and the repulsive modality is the lateral sense. If this conclusion were correct for all species it would be assumed that there were no olfactory responses in the present study during the tests performed in artificial light during daytime. The results arrived at with young char, however, clearly show attraction to the odorous water current in comparison to that free from odour (Figs. 6a, b and 7a, b). Furthermore, this remarkable attraction disappears if the olfactory organs are destroyed by simply burning the olfactory epithelium (Figs. 6c, d and 7c, d). The conclusion is that young char use their olfactory sense to recognize other individuals or a group of the same species which cannot be seen. This is valid even in light; the situation in darkness or at night has not yet been studied. SHAW (1962) states that fishes that cannot see cannot school. One conclusion from our work is that young char that cannot smell have difficulties in recognizing individuals of the same species which are not sighted. Some kind of specific odour or odours synthesized

by the fish — possibly in the skin — seem to be involved in the schooling behaviour shown by the species. From commercial fishery statistics, SOLOMON (1973) presented circumstantial evidence of pheromone-influenced homing by migrating salmon, *Salmo salar*. NORDENG (1971) reported that homing by a migratory population of the char *Salvelinus alpinus*, might be explained by local attraction to schools of this species. According to NORDENG (*op.cit.*), intraspecific or race-specific attractants might be secreted in the mucus. But such odiferous agents have not actually been chemically identified, and furthermore the perceptual background of the above-mentioned field observations, as well as of the reactions demonstrated in the present study, are problems which remain to be solved in future work.

As shown by BARTH (1961), the production of the sex pheromones in an insect is controlled by endocrine mechanisms. Evidence is accumulating to suggest that prolactin maintains or proliferates epidermal mucous cells and that hypophysectomy reduces mucous cells in the gills and in the skin of teleosts (for references see BALL, 1969, p. 219; ALER, 1971, a, b). If this is also true for the salmonids in question here, hypophysectomized and prolactin-treated fish (or fish treated with other hormones) might produce different amounts of pheromones. Then, given a choice between one stream in the fluvium containing odours from untreated individuals and another stream on the opposite side of the test yard containing odours from fish pretreated by hormone injections or hypophysectomy, preference reactions (attraction or avoidance) of different magnitudes might be manifested. Thus, using the present experimental analysis in combination with an endocrinological approach, more reliable proof of possible connections between pheromone synthesis and secretion by mucous cells in fish might possibly be obtained.

V. ACKNOWLEDGMENTS

Our thanks are due to Dr GUNNAR SVÄRDSON and Dr NILS ARVID NILSSON at the Institute of Freshwater Research, Drottningholm, for valuable suggestions on this project. We also thank the Fishery Board of Sweden and Mr NILS G. STEFFNER, Älvkarleby, for supplying the fish material.

VI. SUMMARY

The role of olfaction for communication and schooling behaviour among juvenile char (*Salvelinus alpinus* (L.)) was investigated. Intact fishes showed a strong preference to water currents with intraspecific odours in a choice between one free from smell. The effect disappeared when the olfactory organ was removed although the normal preference to water currents seemed unchanged. The results indicate that olfaction and chemical stimulation play a dominant role in communication (attraction) between individual young char (*S. alpinus* (L.)).

VII. REFERENCES

- ALER, G. M. 1971a. The study of prolactin in the pituitary gland of the Atlantic eel (*Anguilla anguilla*) and the Atlantic salmon (*Salmo salar*) by immunofluorescence technique. *Acta Zool. Stockh.* 52: 145—156.
- 1971b. Prolactin-producing cells in *Clupea harengus membras*, *Polypterus palmas* and *Galamoichtys calabaricus* studied by immuno-histochemical methods. *Acta Zool. Stockh.* 52: 275—286.
- BALL, J. N. 1969. Prolactin (fish prolactin or paralactin) and growth hormone. In Hoar, W. S. and D. J. Randall, Eds. *Fish Physiology* Vol. II. The Endocrine System p. 207—232. Acad. Press. New York and London.
- BARDACH, J. E., and TODD, J. H. 1970. Chemical communication in fish. p. 205—240. In: *Communication by chemical signals*. Appleton-Century-Crofts. Eds: JOHNSTON, J. W., Jr., P. G. MOULTON, and A. TURK. New York.
- BARTH, R. H. 1961. Hormonal control of sex attractant in the Cuban cockroach. *Science*. 133: 1598—99.
- HEMMINGS, C. C. 1966. Olfaction and vision in fish schooling. *J. exp. Biol.* 45: 449—464.
- HÖGLUND, L. B. 1961. The reactions of fish in concentration gradients. *Rep. Inst. Freshw. Res., Drottningholm*. 43: 1—147.
- KARLGRÉN, L. 1962. Vattenkemiska analysmetoder. Inst. Limnol. Uppsala. (Mimeographed in Swedish.) 115 p.
- KLEEREKOPER, H. 1969. Olfaction in fishes. Indiana Univ. Press. Bloomington. 222 p.
- 1971. Orientation through chemoreception in fishes. In: *Nasa-Smithsonian Institution Symposium on Animal Navigation and Orientation, Wallops Islands, 1970*.
- MARCRSTRÖM, A. 1967. Studies on the connection between physicochemical properties and stimulating abilities of some sweet and bitter compounds. *Ark. Zool.* 19(22): 422—532.
- MARLER, P., and HAMILTON, W. 1966. Mechanisms of animal behaviour. Wiley, New York.
- NORDENG, H. 1971. Is the local orientation of anadromous fishes determined by pheromones? *Nature* 233: 411—413.
- SHAW, E. 1962. The schooling of fishes. *Sci. Amer.* 206: 128—138.
- SOLOMON, D. J. 1973. Evidence for pheromone-influenced homing by migrating Atlantic salmon, *Salmo salar* (L.). *Nature* 244: 231—232.
- TODD, J. H., ATEMA, J., and BARDACH, J. E. 1967. Chemical communication in social behaviour of a fish, the yellow bullhead (*Ictalurus natalis*). *Science* 158: 672—673.

The Effect of Cooling Water Discharges on Zooplankton in a Bay of Lake Mälaren

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I. INTRODUCTION

This study is part of a project directed by Dr. ULF GRIMÅS, Swedish Environment Protection Board, Stockholm. The project aims at analysing the effect of cooling water discharges from two fossil fuel power stations in the inner part of the Västerås Bay, Lake Mälaren, Sweden. Apart from zooplankton, constituting the object of the present study, physical and chemical conditions, vegetation, bottom fauna and fish are being investigated by other scientists.

For a description of the area and the background we refer especially to GRIMÅS (in MS) and WIEDERHOLM (1971). It should be mentioned that the bay is affected also by municipal sewage (from the city of Västerås) which is why there are some difficulties in distinguishing the true effect of the cooling water.

The investigation was carried out in March and April 1972 and comprises quantitative as well as qualitative samples (for a closer account, see LANNER 1972). Unfortunately, only net samples were taken from the strip of open water in the ice just outside Aroskraft Power Station, but both net and quantitative samples (5 l sampler according to RODHE 1941) from different depths were collected at other stations (see Fig. 1). In Table 2 these stations are arranged roughly according to their distance from the power stations, the nearest station (no. 12) being the first. At station 12 two simultaneous samples were taken from each depth (I and II) in order to get an idea of the role of randomization. The mesh sizes used were 100 μ (net samples, for crustaceans), 63 μ (quantitative samples) and 25 μ (net samples, rotifers). As far as the quantitative samples are concerned care was taken to ensure that neither crustaceans nor rotifers escaped (the protozoans were not studied).

II. RESULTS AND DISCUSSION

In the strip of open water in the ice outside Aroskraft Power Station the temperature varied rather widely, being 5.8°C at the surface and 4.8°C at 3 m depth in the locality where the netting was made (see Table 1). At the other spots even temperatures above +9°C were measured.

The number of zooplanktic species found in these net samples must be considered as high with respect to the season. Most forms found are eurythermal or coldwater stenothermal according to previous literature (see, e.g., CARLIN 1943 and PEJLER 1957). *Polyarthra remata*, however, constitutes an exception, apparently having never before been found in the middle of the winter. Its purely warm stenothermal occurrence is quite obvious, e.g., from Fig. 141 in CARLIN, *op.cit.*, and from Figs. 23 and 30 in PEJLER, *op.cit.* Quantitative samples were taken at the end of March and at the end of April. During the March investigation pure winter conditions still prevailed, so these samples were chosen for a detailed account, Table 2. From this table it is evident that most species occurred in their highest numbers at station 12, *i.e.* the locality nearest the Power Station. The accumulation is especially obvious for the species of *Synchaeta* and *Polyarthra*. The relatively high frequency of *Asplanchna priodonta* is also of interest: This rotifer has a partly predatory habit and should thus be attracted to the localities where prey is abundant. Most *Asplanchna* individuals contained devoured *Keratella cochlearis* and/or *K. quadrata* in their stomachs. Besides the species found in the open water, *Notholca acuminata* (EHRBG), *Eurytemora lacustris* (POPPE) and *Heterocope appendiculata* SARS were collected in the more distant localities. On the other hand, three species were found only in the strip of open water,

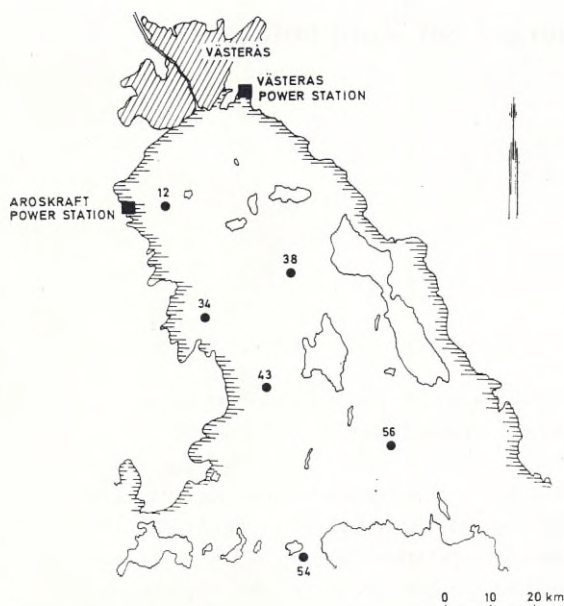


Fig. 1. Map showing the sites of the sampling stations.

Table 1. Composition of the zooplankton in the net samples from the strip of open water in the ice outside Aroskraft Power Station. The crosses indicate relative frequency.

Date	22.III	20.IV
<i>Keratella cochlearis</i> (GOSSE)	+++	++
<i>Keratella quadrata</i> (MÜLL.)	+	++
<i>Keratella hiemalis</i> CARLIN	+	+
<i>Kellicottia longispina</i> (KELICOTT)	+++	++
<i>Notholca squamula</i> (MÜLL.)	+	+
<i>Notholca caudata</i> CARLIN	+	++
<i>Asplanchna priodonta</i> GOSSE	+	+
<i>Synchaeta oblonga</i> EHRBG.	++	+++
<i>Synchaeta pectinata</i> EHRBG.	+	+
<i>Polyarthra vulgaris</i> CARLIN	++	++
<i>Polyarthra dolichoptera</i> (IDELSON)	+++	++
<i>Polyarthra remata</i> (SKORIKOV)	+	+
<i>Filinia terminalis</i> (PLATE)	+	+
<i>Conochilus unicornis</i> ROUSSELET	+	+
<i>Conochiloides natans</i> (SELIGO)	+	+
<i>Daphnia</i> sp.	+	+
<i>Bosmina coregoni</i> BAIRD s.l.	+	++
<i>Bosmina longirostris</i> (MÜLL.)	+	+
<i>Eudiaptomus gracilis</i> (SARS)	++	++
<i>Limnocalanus macrurus</i> SARS	+	++
<i>Cyclops strenuus</i> -group	+++	+++

viz. Notholca squamula, Polyarthra remata and *Bosmina longirostris*. Regarding the copepods, only nauplii were observed in the strip of open water but copepods and adults were found farther away. In addition to the forms noticed in March, *Kellicottia bostoniensis* (ROUSSELET) occurred in a sample from April 19 (Stn 34). It was previously reported from Lake Mälaren by ARNEMO *et. al.* (1968).

III. SUMMARY

A relatively high frequency of species, as well as individuals, was noted in the middle of winter (March 1972) in the inner part of Västerås Bay, which is affected by cooling water discharges from two power stations as well as by municipal sewage from the city of Västerås. In a strip of open water in the ice just outside one of the power stations, where the temperature at some places exceeded $+9^{\circ}\text{C}$, a pronouncedly warmwater stenothermal rotifer occurred, *Polyarthra remata*, previously never found in the winter.

IV. REFERENCES

- ARNEMO, R., B. BERZINS, B. GRÖNBERG, and I. MELLGREN 1968. The dispersal in Swedish waters of *Kellicottia bostoniensis* (ROUSSELET) (Rotatoria). *Oikos* 19: 351—358.
- CARLIN, B. 1943. Die Planktonrotatorien des Motala-ström. Zur Taxonomie und Ökologie der Planktonrotatorien. *Medd. Lunds Univ. limnol. Inst.* 5: 256 p.
- LANNER, M. 1972. Zooplankton i Västerås- och Kungälfjärden; mars och april 1972. *Zool. Inst., Uppsala*. (Mimeographed in Swedish.)
- PEJLER, B. 1957. Taxonomical and ecological studies on planktonic Rotatoria from northern Swedish Lapland. *K. svenska Vetensk. Akad. Handl.*, ser 4, 6(5): 68 p.
- RODHE, W. 1941. Zur Verbesserung der quantitativen Planktonmetodik nebst Profilen des Crustaceenplanktons aus drei smäländischen Seen. *Zool. Bidr. Uppsala* 20: 465—477.
- WIEDERHOLM, T. 1971. Bottom fauna and cooling water discharges in a basin of Lake Mälaren. *Rep. Inst. Freshw. Res., Drottningholm* 51: 197—214.

Table 2. Number of ind./5 l of the most common rotifer species, total Rotatoria and total Copepoda (no cladocerans were found in the quantitative samples) on March 20, 1972. From station no. 12 parallel samples were taken (I and II). Temperatures in degrees centigrade according to measurements by Mr. CHRISTER JOHNSON, SMHI (Swedish Meteorological and Hydrological Institute).

Station no.	12		34		38		43		54		56					
	0.5 I	2 II	0.5 I	2 II	5 I	10 II	5 I	10 II	0.5 I	13 II	5 I	10 II	0.5 I	13 II	5 I	10 II
Depth in metres	0.25	—	1.77	—	1.35	1.60	1.75	1.48	1.58	1.77	—	—	0.79	0.84	1.68	2.56
Temperature	93	63	129	—	44	39	21	33	29	14	12	—	21	31	10	13
<i>Keratella cochlearis</i>	9	8	4	9	4	—	4	—	4	2	1	—	2	4	1	2
<i>Keratella quadrata</i>	8	16	10	22	5	5	14	9	4	5	6	—	—	—	4	2
<i>Kellicottia longispina</i>	4	3	1	2	—	—	—	—	—	—	—	—	—	—	—	—
<i>Asplanchna priodonta</i>	15	31	20	16	—	2	—	1	1	3	—	—	—	—	—	—
<i>Synchaeta oblonga</i>	2	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Synchaeta pectinata</i>	14	10	11	17	4	4	—	2	4	—	—	—	—	—	—	—
<i>Polyarthra vulgaris</i>	60	20	28	59	—	—	1	1	—	—	—	—	7	2	—	—
<i>Polyarthra dolichoptera</i>	206	157	137	255	59	51	42	46	44	22	23	—	37	37	15	17
total Rotatoria	149	84	96	203	95	113	79	96	126	54	57	—	30	33	29	66
total Copepoda (all stages)	355	241	233	458	154	164	121	142	170	76	80	—	67	70	44	83
total zooplankters																

On the Vertical Distribution of Oligochaetes in Lake Sediments

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I. INTRODUCTION

The availability of bottom invertebrates as food for fish has long been a question of primary interest to fishery biologists. To what extent are deep-burrowing animals like worms and some chironomid larvae available in this context? There is no doubt, however, that fish will readily take worms if they are offered.

The vertical distribution of the benthos is also of great importance in relation to its influence upon the circulation of matter in the body of water (cf. TESSENOW, 1964; EDMONDSON and WINBERG, 1971). The activities of benthic organisms have not often been thought of in terms of regeneration of material and energy from the sediments (BRINKHURST, 1972).

In order to get better information on the vertical distribution of oligochaetes and to a lesser extent other invertebrates, in lake sediments the author once found it necessary to construct a new sampling device adopting a new technique, *i.e.* thin metal slides which instantly divided an unbroken mud-water core into thin layers once the sampler had reached the desired depth in the sediments (MILBRINK, 1968).

In this way very mobile animals like several crustaceans, chironomid larvae, *Chaoborus* larvae, some oligochaetes etc. are prevented from making any larger vertical movement after sampling. The whole process is a matter of tenths of a second, provided the release wire is tight enough.

Vertical displacement of the more motile species can not be determined unless the sectioning of the core commences immediately after collection (COLE, 1953, *cf.* also LENZ, 1931; BERG, 1938; BRINKHURST and KENNEDY, 1965; SÄRKKÄ and PAASIVIRTA, 1972).

The author is not aware of the existence of any similar bottom sampler. In the author's opinion the vertical distribution of the entire bottom community is worth closer study. Physical-chemical measurements have also been made in addition to the different zoological data given by this technique (MILBRINK, 1969).

This micro-stratification technique has successfully been transferred to potentiometric measurements, to studies of bacteria and organic matter in the mud etc. by Dr. J. OLÁH and Dr. A. FRANKO, Hungary (unpublished material; some results kindly put at the author's disposal. Results will shortly be published in *Annal. Biol. Tihany, Hungary*).

The purpose of the present paper is, in first hand, to illustrate and discuss the vertical distribution of oligochaetes with reference to a selected area in Hovgårdsfjärden in central Lake Mälaren.

II. GENERAL BACKGROUND

The Lenz-Ekman sampler was an important means towards the understanding of the vertical distribution of the fauna in lake sediments. Metal shelves were inserted through slots in an ordinary, but tall, Ekman-sampler thereby dividing the mud-water core into strata. However, the very insertion was not made until the filled sampler had reached the water surface again. Naturally, there is always some chance that mobile animals have already been able to displace themselves vertically, a fact which would make such samples more or less useless for this purpose (cf. LENZ, 1931; BERG, 1938; SÄRKKÄ and PAASIVIRTA, 1972).

The same disadvantage is also valid for corers of different kinds. The time lapse is often too long before sectioning of the core starts. Even the

deep-freezing method described by EFFORD (1960) is probably far too slow.

It is also difficult to avoid compression or expansion or other displacement of the sediments if the core is fetched from some depth (*cf.* EDMONDSON and WINBERG, 1971). Of course, the effects of such changes of the core are largely reduced if the core is already divided before the changes commence *i.e.* before the sampler is removed from the sediments.

LENZ' sampling technique was later adopted by BERG (1938) and BORUTSKY (1935, 1940) with minor modifications, mostly concerning the distance between the shelves. The recommendations in EDMONDSON and WINBERG (1971) are evidence that the technique is still widely used.

These samplers have been used for different purposes, for instance, by DEKSBACH (1939), KIRPICHENKO (1940), PODDUBNAYA (1961), PODDUBNAYA and SOROKIN (1961), PATARIDZE (1967), KJÄLLMAN and GRIMÅS (1967), and SÄRKKÄ and PAASIVIRTA (1972).

Another box sampler constructed on much the same working principle is the Digerfeldt-Lettevall sampler (DIGERFELDT and LETTEVALL, 1969). Accordingly the shelves are inserted after the sampler returns to the water surface. The sampler is tall which is an advantage on very loose bottom material and it is transparent for a better localization of the different sediment strata and in particular the mud-water interface. Special varieties of the above are the hand directed samplers by FORD (1962) and FAGER (1966).

Modern core samplers with transparent tubes of plexiglass like the Kajak sampler, the simplified corer described by the author (MILBRINK, 1971) and several others, provide fairly undisturbed mud-water cores which can be subdivided with the piston technique designed for the well-known Jenkin sampler (MORTIMER, 1941/1942). The Elgmork sampler is also a useful device on very loose bottom material (ELGMORK, 1962).

A great number of corers and samplers, some of them suitable for microstratification studies, are presented in HOPKINS (1964), EDMONDSON and WINBERG (1971), and to some extent in MILBRINK (1971). Most corers with narrow openings seem to be designed primarily for micro-fauna studies, for which purpose they operate quite satisfactorily.

At the moment there is also a growing interest in hand-taken cores (the SCUBA technique). Tube samplers are recommended for microstratification studies by BRINKHURST and JAMIESON (1971).

The coring technique, however, must be handled very carefully since if the tube is not wide enough the friction of the core against the walls may be considerable. Accordingly there will always be a risk that the sediment strata get partly mixed (*cf.* EDMONDSON and WINBERG, 1971).

Some of the above works have been more or less focused upon the vertical distribution of oligochaetes, *i.e.* PODDUBNAYA (1961), PODDUBNAYA and SOROKIN (1961), BRINKHURST and KENNEDY (1965), PATARIDZE (1967), BRINKHURST *et al.* (1969), and SÄRKKÄ and PAASIVIRTA (1972).

III. MATERIAL AND METHODS

The ultimate aim of the study presented first (Fig. 2) was to acquire thorough information on the vertical as well as the horizontal distribution of oligochaetes — and other invertebrates — referring to the particular date of sampling. The area selected was Hovgårdsfjärden in the central — *i.e.* the cleanest — parts of Lake Mälaren, the bottom fauna of which is well-known to the author.

The area was visited by G. ALM in 1915—1916, by S. VALLIN in 1933, by T. WIEDERHOLM in 1969—1970, and by the present author in 1970 and 1971. The oligochaete material of these surveys has remained preserved to the present-day. A paper on the oligochaete fauna of Lake Mälaren covering this material is in preparation.

The bottom area selected is absolutely flat and sheltered and considered homogeneous in most respects, for instance in texture, bottom fauna composition (MILBRINK, 1972), exposure to wave actions, streams etc. Thus it is among the best possible areas for the purpose. The depth is 32 m and the width about 2×6 km². The time of sampling was August 1970.

In order to obtain enough information on both the vertical and the horizontal aspects several parallel microstratification samples had to be taken. Since each sample of this kind means the necessary acquirement of a great number of subsamples and much labour is involved preparing the

sampler for each core, it is generally not realistic to take more than two or three parallel samples a day, which is naturally a drawback in terms of representativity. In combination with 5–10 Ekman samples or some 10–20 tube samples, however, a fairly accurate picture of the horizontal aspect is usually secured.

In Hovgårdsfjärden seven microstratification samples and one Ekman sample — all obtained in one day — were spread radomly in the grid measuring 100×50 m². The same grid was later used (in March 1971) in a special study on the horizontal distribution of the bottom fauna (MILBRINK, 1972), when 48 samples were similarly spread in the net.

Each of the other four examples given below describes the results from 2 or 3 microstratification samples in combination with ordinary Ekman samples and has been selected because here the oligochaete material was analysed in detail. Such analyses are generally extremely time-consuming, since the majority of worms are immature. The selected samples primarily serve as examples of the vertical distribution of oligochaetes from various habitats and will to some extent modify the general picture obtained in Hovgårdsfjärden.

The second example given below is from Norra Björkfjärden — also in central Lake Mälaren. The samples were obtained from a depth of 30 meters in September 1967. The third example is from Ekoln, a much enriched basin in northern Lake Mälaren — the depth being 32 meters and the time of year February 1968; the fourth from Lake Erken, a eutrophic lake to the east of Uppsala near the Baltic — the depth being 18 meters and the time of year June 1968; the fifth and last also from Lake Erken and the time of year August 1968.

It must be emphasized that the above examples merely represent the momentary distributions of organisms.

The bottom material was generally very lightly sieved through a 0.3 mm sieve, while the water-containing chambers were tapped through bags of nylon gauze with 0.06 mm meshes. All sediment residues were examined as soon as possible without foregoing preservation. In the first test described below, however, preservation liquids were added to the residues of four samples.

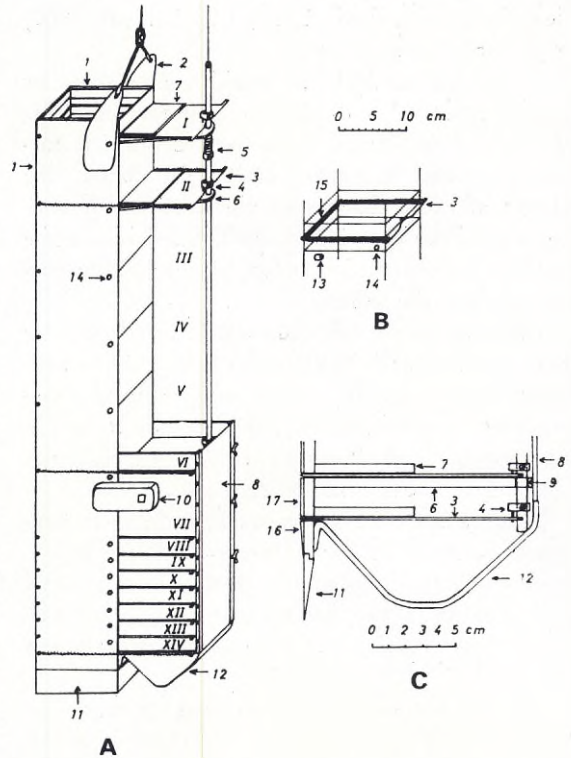


Fig. 1 A and B scale roughly 1:11, Fig. 1 C scale roughly 1:4. The slide mechanisms for Nos. III, IV, and V and most of the springs are omitted from the drawings. Fig. 1 B is a more detailed sketch of the fitting of the slide between runners of plexiglass. At the bottom is a shock absorber of 1 mm brass (15). Fig. 1 C a transverse section through the lower part of the "slide-box". 1. The tube of 6 mm plexiglass 2. the suspensions, brass plates and steel wire. 3. slide of 1.5 mm duraluminium 4. movable hooks on a rod (of 9 mm brass) which is spring-loaded (5). 6 and 7. supports of 6 mm plexiglass with brass bearings (9) for the rod 8. hinged lid to the "slide-box" 10 exchangeable lead weights 11. exchangeable brass edge 12. streamline protection cone made of plexiglass 13. spout of plexiglass 14. hole with a plug for the chamber 15. brass plate for shock absorbtion 16. bevelled runner of plexiglass 17. runner of plexiglass (2 mm).

The results are illustrated in a manner which may need some explanation. The diagrams (Figs. 2–6) are composed of smaller units each representing the abundance of a group (or other entity of bottom invertebrates) or individual species per vertical centimetre of the core.

Precision varies between the different investi-

gations depending upon the actual number of parallel samples obtained each time. In Figs. 2, 4, and 6 the exactitude of vertical localization of animals is calculated to be ± 0.5 cm, while in Figs. 3 and 5 it is only ± 1.25 cm.

These intervals of precision are the natural consequences of the chosen distance between parallel slides of the microstratification sampler (2.5 cm) and the number of samples obtained. Accordingly the obvious lack of continuity in the vertical distribution of some species (or other entities of animals) is not necessarily real.

Brief description of the sampler (see Fig. 1)

The sampler is built of 6-mm plexiglass, the tube has a square cross-section measuring exactly $1/60$ m² (167 cm²) — in order to simplify the estimation of specimens per square metre unit.

The slide box and the protection cone built of plexiglass of varying thickness are considered necessary to reduce turbulence in front of the device. The slide box is easily dismantled in the field which facilitates the changing of slides.

The slides are made of 1.5 mm duraluminium, a hard, elastic, and very light material. They are loaded with slender springs of stainless steel placed outside the tube.

For the purpose of these studies a distance of 2.5 cm was chosen on empirical grounds to separate the lower slides, while further up 10 cm was considered appropriate.

The closing mechanism is operated from the water surface by means of a thin wire. As mentioned before the whole releasing procedure takes a matter of a few tenths of a second, a fact which makes it difficult even for mobile animals to move much vertically.

For further details the reader is referred to MILLBRINK (1968).

IV. RESULTS

Horizontal distribution

The microstratification samples from Hovgårdsfjärden also gave information on the horizontal distribution. It emerges from Tables 1 and 2 that

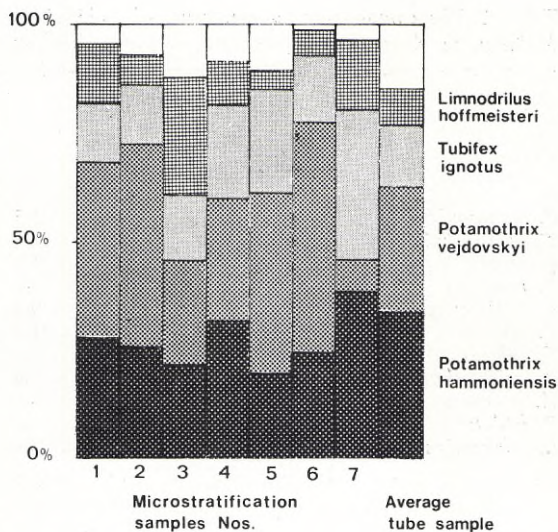


Table 1. The composition (in per cent) of Tubificidae in bottom samples obtained in Hovgårdsfjärden, Lake Mälaren, in August 1970 (separate microstratification samples) and in March 1971 (an average tube sample).

the qualitative composition of tubificids had not changed markedly from August 1970 to March 1971. The same species dominated in approximately the same proportions. The only tubificid having changed notably was *Tubifex tubifex*, which had increased from 1 to 11 per cent. This "change", however, is not necessarily real as *T. tubifex* and *T. ignotus* may be very difficult to separate properly from each other in their youngest stages. At the same time *T. ignotus* had actually decreased from 20 to 14 per cent.

Ten tubificid species were common to both studies; only *Limnodrilus udekemianus* having been replaced by the closely related *L. claparedeanus*.

In each microstratification sample the four major components made up at least 88 % of the whole tubificid population (see Table 1). The study in March revealed that the same four dominating species made up 84.5 % of all tubificids. When looking more closely at the contents of oligochaetes of different species in each sample (Ekman or microstratification sample) it must be remembered that an ordinary Ekman sampler takes 1.3–1.5 times more bottom material than the other sampler *i.e.* in proportion to its larger aperture (Table 3).

Table 2 The composition (in per cent) of Tubificidae in bottom samples obtained in Hovgårdsfjärden, Lake Mälaren, in August 1970 (separate microstratification samples) and in March 1971 (an average tube sample).

	Microstratification samples							mean	Average tube sample
	1	2	3	4	5	6	7		
<i>P. hammoniensis</i>	27.3	25.3	21.2	31.5	19.5	24.7	38.4	26.8	34.0
<i>P. vejdotskyi</i>	40.9	47.0	24.2	28.3	41.5	52.8	7.4	34.6	28.0
<i>P. ferox</i>	2.3	—	6.2	1.1	—	—	—	1.4	2.0
<i>P. barbatus</i>	—	—	3.0	—	—	1.0	—	0.6	1.0
<i>L. hoffmeisteri</i>	13.6	6.9	27.2	9.8	3.7	5.4	16.0	11.8	8.5
<i>T. ignotus</i>	13.6	13.8	15.2	21.7	24.3	15.0	34.5	19.7	14.0
<i>T. tubifex</i>	—	—	3.0	—	3.7	1.1	—	1.1	11.5
<i>B. vejdotskyanum</i>	2.3	3.9	—	7.6	4.9	—	3.7	3.2	<1
<i>A. pluriseta</i>	—	3.1	—	—	—	—	—	0.4	<1
<i>P. bedoti</i>	—	—	—	—	1.2	—	—	0.2	<1
<i>L. udekemianus</i>	—	—	—	—	1.2	—	—	0.2	<1
	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Table 3. Relative abundance of different Oligochaeta in eight bottom samples from Hovgårdsfjärden, Lake Mälaren, in August 1970. Single specimens are indicated with one X. More than 4 specimens/sample are marked with XX.

	Ekman sample	Microstratification samples Nos.							Frequency	
		1	2	3	4	5	6	7		
TUBIFICIDAE										
<i>Potamothenis hammoniensis</i>	XX	XX	XX	XX	XX	XX	XX	XX	XX	in all samples
<i>Potamothenis vejdotskyi</i>	XX	XX	XX	XX	XX	XX	XX	XX	XX	in all samples
<i>Pelosclex ferox</i>	X	X	—	X	X	—	—	—	—	
<i>Psammorectides barbatus</i>	—	—	—	X	—	—	X	—	—	
<i>Limnodrilus hoffmeisteri</i>	XX	XX	XX	XX	XX	XX	XX	XX	XX	in all samples
<i>Tubifex ignotus</i>	XX	XX	XX	XX	XX	XX	XX	XX	XX	in all samples
<i>Tubifex tubifex</i>	—	—	—	X	—	X(X)	X	—	—	
<i>Bothrioneurum vejdotskyanum</i>	XX	X	XX	—	XX	XX	XX	XX	XX	in all samples but one
<i>Aulodrilus pluriseta</i>	XX	—	X	—	—	—	—	—	—	
<i>Potamothenis bedoti</i>	—	—	—	—	—	X	—	—	—	
<i>Limnodrilus udekemianus</i>	—	—	—	—	—	X	—	—	—	
Total number of species	7	6	6	7	6	8	7	5		
NAIDIDAE										
<i>Vejdotskyella comata</i>	XX	XX	XX	XX	XX	XX	XX	XX	XX	in all samples
<i>Speciaria josinae</i>	XX	XX	XX	XX	XX	XX	XX	XX	XX	in all samples
<i>Stylaria lacustris</i>	X	X	XX	XX	XX	XX	X	X	X	in all samples
<i>Piguetiella blanci</i>	X	—	X	X	—	X	X	X	X	
<i>Uncinaiis uncinata</i>	XX	XX	XX	X	XX	—	XX	X	X	in all samples but one
<i>Nais</i> sp.	X	—	—	—	X	—	—	X	—	
<i>Arcteonais lomondi</i>	XX	—	—	—	X	—	XX	—	—	
<i>Pristina</i> sp.	X	—	—	—	—	—	—	—	—	
<i>Vejdotskyella intermedia</i>	—	X	—	—	—	—	X	—	—	
<i>Chaetogaster cristallinus</i>	—	—	—	—	—	—	X	—	—	
AELOSOMATIDAE										
<i>Aelosoma</i> sp.	—	—	—	—	X	—	—	—	—	
Total number of species:	8	5	5	5	7	4	8	6		

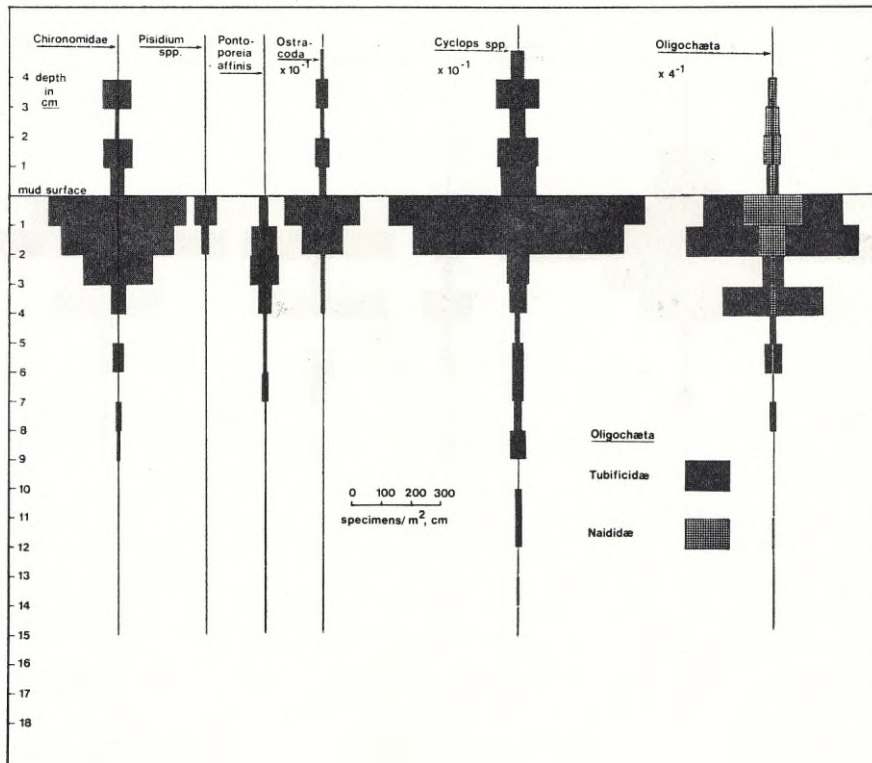


Fig. 2: 1. (Hovgårdsfjärden).

The Ekman collected 7 tubificid species, while none of the m-samples (microstratification samples) contained less than 5. The mean value was 6.4. Similarly the Ekman took 8 naidid (and aeolosomatid) species. The m-samples varied between 4 and 8 with a mean value of 6.

The four dominating tubificid species were represented — even well-represented — in all samples. A fifth species was represented in all samples but one. Similarly two naidid species were well-represented in all samples, a third species was represented in all samples, and a fourth in all but one. Of a total number of 22 oligochaete species the Ekman took 15 and the m-sampler between 11 and 15, with a mean value of 12.

In fact, most bottom fauna constituents were rather evenly spread over the grid judging from these comparatively few samples, e.g. chironomid larvae had a mean value (\pm standard deviation) of specimens/m² of 1584 (\pm 420), *Pontoporeia affinis* (264 \pm 108), and oligochaetes 6660 (\pm 1776).

Vertical distribution

Even if stress here has been laid upon the vertical distribution of oligochaetes in general — and the Hovgårdsfjärden material in particular — the author has considered it desirable to illustrate the distributions of the other main constituents as well.

An adverse relationship between numbers of chironomid larvae and tubificid oligochaetes has, for instance, been presumed by BRINKHURST and KENNEDY (1965) and JÓNASSON (1972).

Hovgårdsfjärden

Important bottom fauna constituents in the Hovgårdsfjärden material (Fig. 2) were chironomid larvae, oligochaetes, pisiids, *P. affinis*, nematodes, and small crustaceans like ostracods and copepods. Naturally, several other groups were represented as well, such as Hydracarina, Ephemera, *Corethra* larvae, hydras etc., even if all those groups are not illustrated in the diagrams. Most of the last-

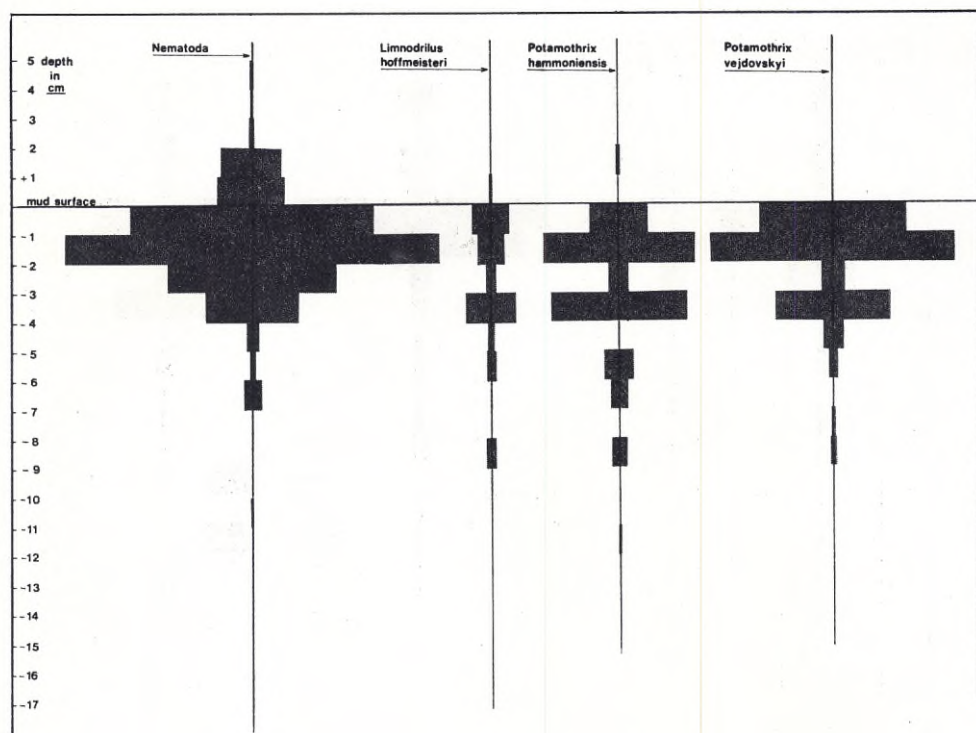


Fig. 2: 2. (Hovgårdsfjärden, continued).

mentioned animals were concentrated at the mud-water interface, or even above it, either as a consequence of undue turbulence acting upon very light organisms at the moment of sampling or as a consequence of spontaneous, swimming movements.

Most chironomid larvae (Fig. 2) were concentrated in the top centimetres of the mud core — some obviously dwelling in funnels of clay at the interface; a minority of larvae were found deeper, and some even above the interface (mostly belonging to the family Tanyptodinae).

Pisidium spp. were also recorded at the interface and so were most ostracods. *Pontoporeia affinis*, on the other hand, was most numerous at depths varying between 1 and 3 cm in the sediments, which is in good agreement with the author's experience. The species may be dwelling there out of nutritional reasons, but it is also quite plausible that it is an avoidance reaction against the approaching sampler (cf. discussion below). Similarly, one *Corethra* larva was found between 4 and 6.5 cm in the mud (cf. discussion). *Cyclops* spp. were,

as usual, the deepest burrowing organisms, even if — as here — the bulk of organisms were found at the interface.

On the whole, naids were well separated from tubificids vertically. Some species of Tubificidae were also well separated from others (see below). SÄPKAREV (1959) and BRINKHURST *et.al.* (1969), for instance, found few, if any, indices of a vertical separation of different tubificid species (see discussion below). Judging from the samples from Hovgårdsfjärden and the other m-samples, *Limnodrilus hoffmeisteri* and *Potamothenrix hammoniensis* are generally the deepest burrowing tubificids (see further text). In the author's experience *Potamothenrix vejdotskyi*, *T. tubifex*, and *Potamothenrix heuscheri* (see below) also burrow deeply. *L. hoffmeisteri* is generally fairly evenly spread through the mud column with rather undistinct maxima of abundance.

In the Hovgårdsfjärden samples *L. hoffmeisteri*, *P. hammoniensis*, and *P. vejdotskyi* were recorded deepest in the mud (to a depth of about 10 cm).

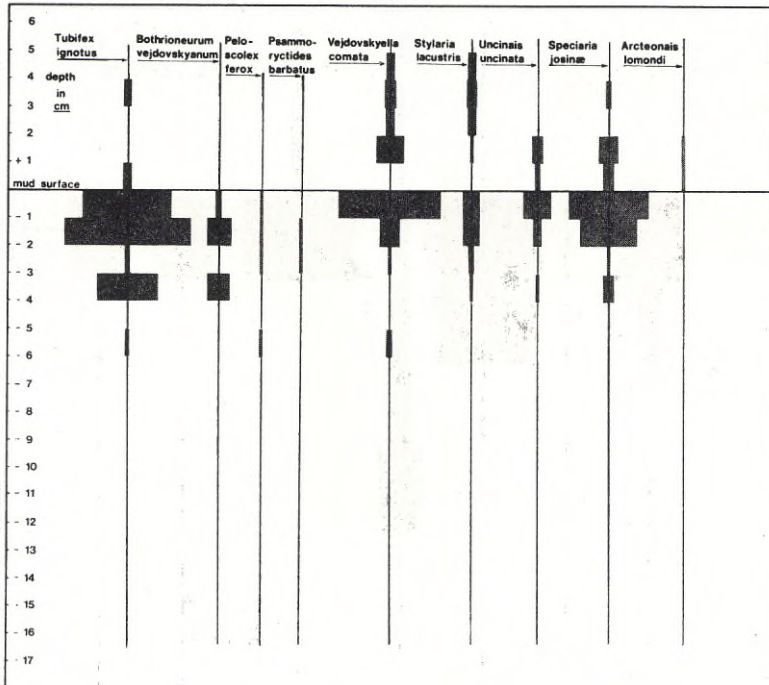


Fig 2: 3. (Hovgårdsfjärden, continued).

The two former species, however, seemed to have their maxima of abundance slightly lower than the latter species and *Tubifex ignotus*. The remaining tubificid species, i.e. *Bothrioneurum vej dovskyanum*, *Peloscolex ferox*, *Psammoryctides barbatus*, *Potamothrix bedoti*, and *Aulodrilus plurisetus* were all recorded in the topmost sediment layers, but since the number of specimens obtained of each species was rather limited it is hardly possible here to say anything definite about the vertical preferences of those species.

On the whole there were very few naidids recorded below a mud depth of about 2 centimetres. The deepest recorded species were the ones illustrated in Fig. 2: 3. The remaining six naidid species were all found superficially in the mud or immediately above it.

The composition of tubificids confirms the general opinion that the water in Hovgårdsfjärden is of good quality. *P. ferox* and *P. barbatus* do not appear at all in polluted areas of Lake Mälaren, i.e. in waters with decreased concentrations of oxygen in water strata close to the bottom. Ac-

cordingly the species are confined to the central basins of the lake (cf. MILBRINK, 1973).

Norra Björkfjärden

The second example on the vertical distribution of oligochaetes was also fetched from the central basins of Lake Mälaren, i.e. Norra Björkfjärden (see above). This material was also used as an example in MILBRINK, 1968 and 1969. The general picture of distribution of the fauna sketched for Hovgårdsfjärden is also valid here (Fig. 3).

Chironomid larvae were concentrated at the mud-water interface, most of the larvae being *Micropsectra* sp. Pisiids, nematodes and weakly built crustaceans like cladocerans and ostracods were all found superficially in the mud, while most *Cyclops* spp. were recorded deeper, i.e. between 4 and 9 cm.

Tardigrada is only one example of a category of bottom invertebrates more or less bound to the interface.

Two tubificid species, *P. hammoniensis* and *L.*

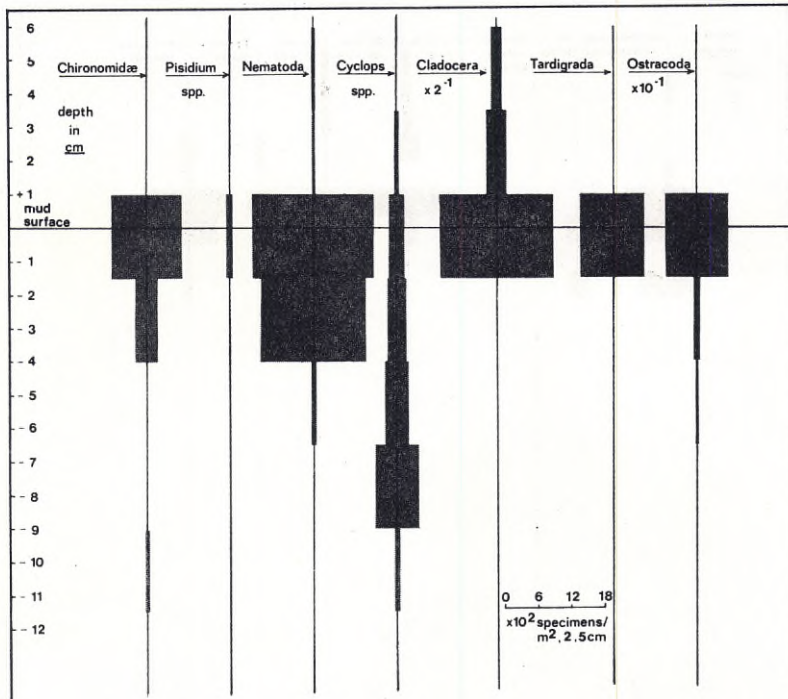


Fig. 3: 1. (Norra Björkfjärden).

hoffmeisteri, and seven naidid species, two of which, *Vejdovskyella intermedia* and *V. comata*, are illustrated in Fig. 3 were well separated vertically with naidids (without exception) occurring in the topmost centimetres of the core and tubificids burrowing deeper (cf. MILBRINK, 1969). Here, too, *L. hoffmeisteri* was rather evenly spread through the column in contrast to *P. hammoniensis* (cf. also Fig. 2).

Ekoln

A winter situation from the Ekoln basin, Lake Mälaren, is the third example (Fig. 4). Larvae of *Chironomus anthracinus* were spread from the surface down to depths of about 5 cm, i.e. about as deep as the deepest penetrating tubificids. Pisiids and ostracods were concentrated at the mud surface, while *Cyclops* spp. were the deepest penetrating organisms (at least 7–8 cm deep), possibly in dormant stages (cf. ELGMORK, 1959).

Tubificids were the almost totally dominating

bottom inhabitants. Naidids (i.e. *Pristina* sp.) were few, possibly depending upon the time of the year. There seems to be little doubt that the tubificid species here were separated vertically. The top layers of the sediments were largely dominated by *P. heuscheri*, the next few centimetres rather equally inhabited by *P. heuscheri*, *P. hammoniensis*, and *T. tubifex*. Strata between 4 and 6 cm were in their turn dominated by *P. hammoniensis*. Characteristically enough, *L. hoffmeisteri* was rather equally distributed through the entire column. The vertical preferences of *P. bedoti* and *T. ignotus* seem here to be vague. The specimens of *A. pluri-seta* were distributed superficially in the mud, which is in accordance with earlier statements about the species.

Both the specific compositions of oligochaetes and chironomid larvae and the quite superficial distribution pattern of most bottom animals except copepods suggest a rather poor oxygen situation at the interface. The Ekoln basin is one of the most polluted basins of Lake Mälaren.

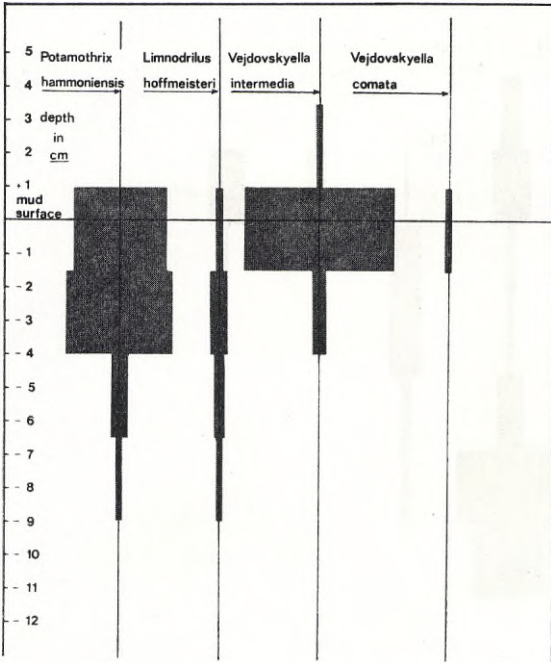


Fig. 3: 2. (Norra Björkfjärden, continued).

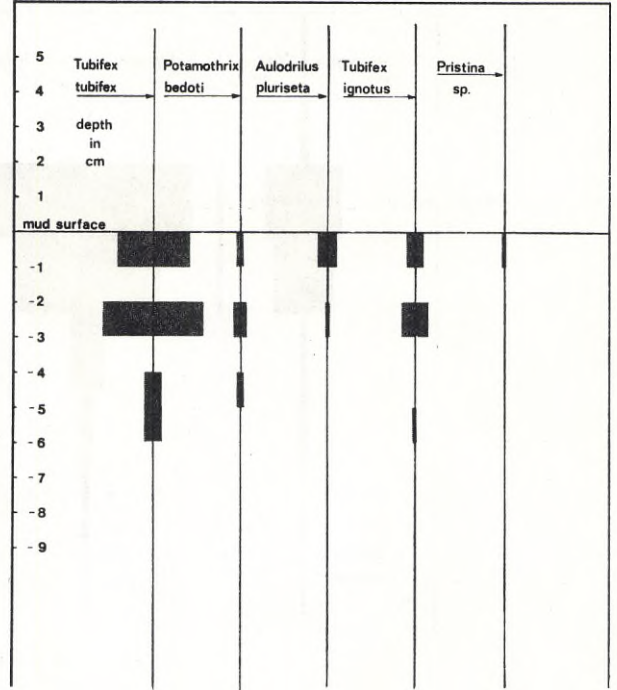


Fig. 4: 2. (Ekoln, continued).

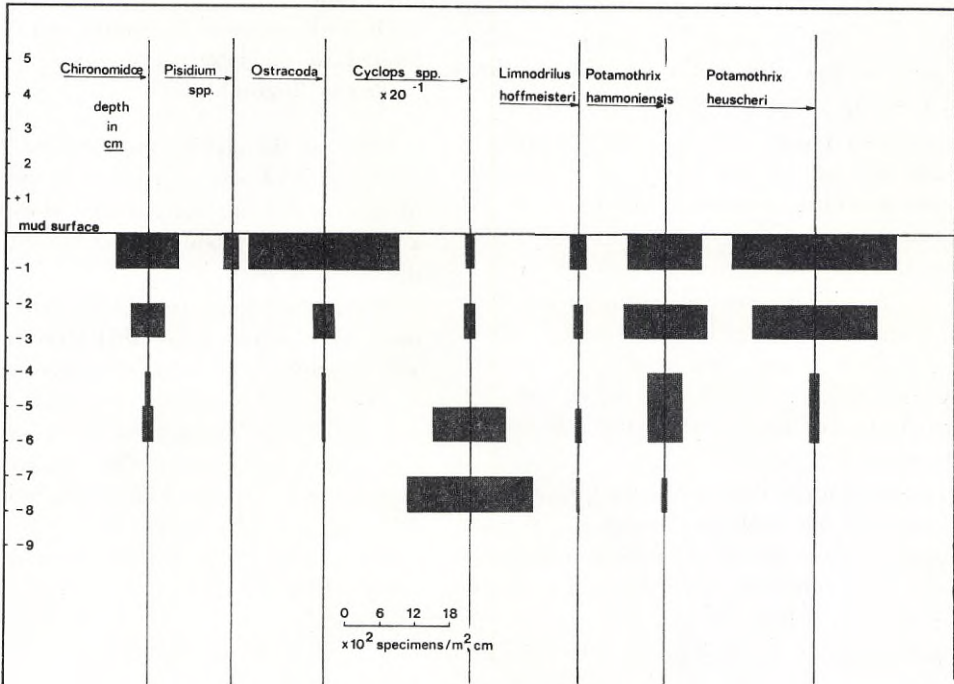


Fig. 4: 1. (Ekoln).

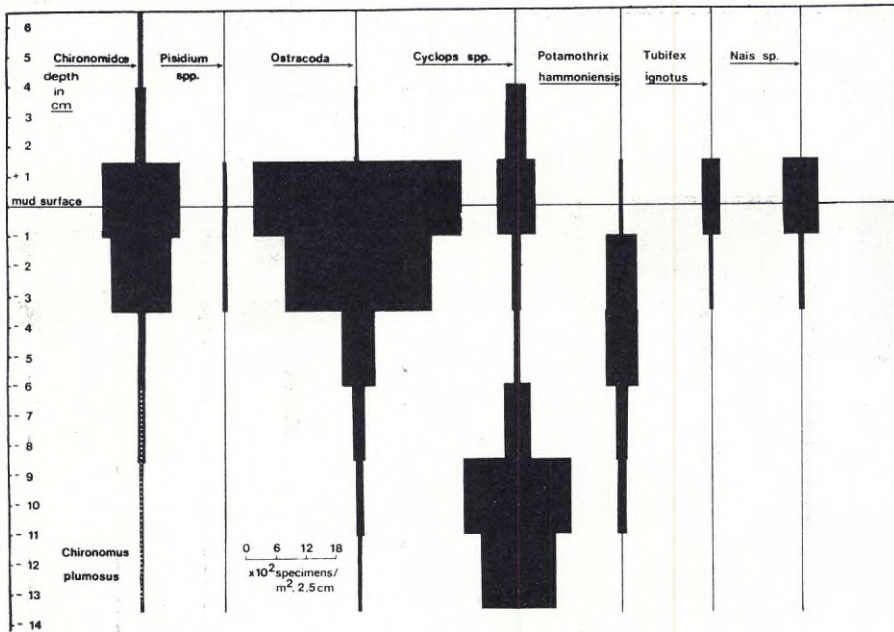


Fig. 5. (Lake Erken, June 1968).

Lake Erken

The last two examples are fetched from the same locality in Lake Erken, the first from June and the last from August 1968. The vertical distribution pattern was almost the same both times (Figs. 5 and 6).

Chironomid larvae were here easily separable into two groups, *i.e.* big larvae of *Chironomus plumosus* dwelling between 5 and 15 cm in the mud and the rest with a maximum of abundance close to the interface.

In August pisiids were located much deeper in the sediments than is generally the case. As a rule most pisiids are found close to the interface (*cf.* above), but BERG (1938), on the other hand, recorded them very deep in the loose sediments of Lake Esrom.

On both occasions ostracods were spread deeper than usual in the mud (*cf.* above) and *Cyclops* spp. displayed maxima of abundance at depths of about 10 cm. Numbers of specimens were found even at depths of about 15 cm.

P. hammoniensis had slightly dissimilar distribution patterns on the two occasions. In August great concentrations of mostly young stages of the

species were concentrated at the interface, while in June the maximum of abundance lay between 2 and 6 cm.

On both occasions *T. ignotus* and *Nais* sp. were limited to the interface and so was *Aulodrilus pigueti* in August.

Three of the dominating tubificid species from Hovgårdsfjärden were tested as to the proportions of mature and immature worms above and below a mud depth of about 3—4.5 cm (*cf.* Fig. 7 and discussion below).

There is no doubt that there were considerably more adult worms below that level than above it. The proportion of sexually mature specimens of *P. hammoniensis* below that level were on an average (seven m-samples) 23 % compared to 7 % above it. Similarly, the relations for *P. vejvodskyi* were 48 % and 26 % respectively and for *L. hoffmeisteri* 70 % and 15 % respectively. Accordingly there were at least about twice as many adult worms of each species below that level as above it.

Similar results, although sometimes less obvious, have been obtained by the author in previous tests with this technique in different waters.

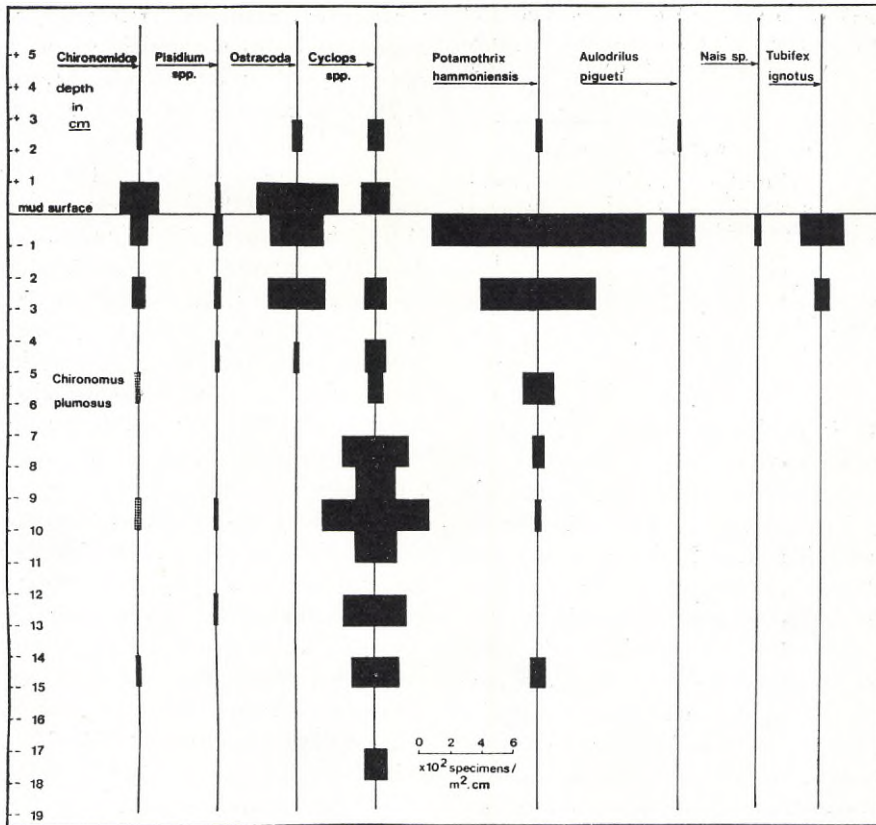


Fig. 6. (Lake Erken, August 1968).

V. DISCUSSION

The extent to which oligochaetes are available to fish is a question which never seems to get a definite answer. East-European authors like PODDUBNAJA (1961), POPCHENKO (1971), GALINSKY and NIKITIN (1972), and YAROSHENKO *et al.* (1972) present evidence that a great number of species of fish, esp. "coarse fish", actively feed on oligochaetes. There is little doubt that "suckers" like bream (*Abramis brama* (L.)), dace (*Leuciscus leuciscus* (L.)), and carp feed most intensively upon tubificids. KENNEDY (1969) and KENNEDY and WALKER (1969) come to the same conclusions from a parasitological approach.

GRIMÅS (1963) discusses the availability of the bottom fauna to fish, especially salmonids. Similar considerations were previously made by NAUMANN (1930), ALLEN (1942), RICKER (1952), and HAYNE

and BALL (1956). GRIMÅS concluded that salmonids in general are poor consumers of oligochaetes.

Nevertheless there are exceptions. Recently brown trout turned out to be an important predator upon the lumbricid *Eiseniella tetraedra* Savigny in impounded lakes in Norway (AAREFJORD *et al.*, 1973). *Coregonus lavaretus* fed most intensively and unselectively upon tubificids in pulp mill fibre banks at depths of about 100 metres in Lake Mjösa, Norway (P. Aass kindly put material at the author's disposal) etc.

The question seems to focus upon the extent to which the worms are exposed to predators like fish. Very agile animals or even swimming ones are certainly of the greatest interest to most fish. *E. tetraedra*, for instance, is a tremendous swimmer when threatened as is evident from aquarium experiments performed by the author (unpubl. material). Its former name *Lumbricus agilis* Hoff-

Fig. 7. Proportions (in per cent) of mature worms of three of the dominating tubificid species in Hovgårdsfjärden above and below a mud depth of about 3—4.5 cm.

mud depth	dominating tubificid species		
	<i>P. hammonsiensis</i>	<i>P. vej-dovskyi</i>	<i>L. hoffmeisteri</i>
topmost			
3—4.5 cm	7	26	15
below a depth of			
4—4.5 cm	23	48	70

meister, 1843 is further evidence of the rapid movements of the species.

Naidids are not seldom encountered in stomachs of various fish especially in fish with littoral feeding habits, which may be linked to the fact that naidids sometimes tend to appear in swarms littorally, thereby being more accessible to fish. *Stylaria lacustris*, *Uncinaiis uncinata* and other naidids are sometimes identified in stomach contents of whitefish and other fish in Sweden. *Paranais litoralis* is at times an important food item for flounders and plaice in Danish estuaries (MUUS, 1967) etc. Most naidids, however, are very inconspicuous and easily overlooked in an ordinary stomach analysis.

Several naidids (e.g. *Stylaria lacustris*) are good swimmers (cf. SPERBER, 1948), but also immature tubificid worms (e.g. *Potamothrix heuschleri*) are definitely capable of swimming freely for short distances if compelled (MILBRINK, unpubl. material). BRINKHURST (1969) denies this capacity of tubificids.

GRIGELIS (1966) presents evidence that proteins are particularly concentrated in the tails of tubificid worms. If oxygen conditions are poor the worms are more or less compelled to expose more of their rear ends than needed for normal purposes (ALSTERBERG, 1925), thereby being more exposed to fish. This means that if fish snap the rear ends of the worms they will get a highly concentrated source of nourishment (cf. PODDUBNAJA, 1962). Accordingly it is not surprising that cypripinid fish in particular snap the respiring ends of tubificids.

The distribution of oligochaetes and other invertebrates in the sediments may very well be a

function of nutritional preferences, but the deep migrations by some tubificid species may also be related to their specific state of maturity according to PODDUBNAJA and SOROKIN (1961) and SOROKIN (1966).

In BRINKHURST and CHUA (1969), BRINKHURST and JAMIESON (1971), WAVRE and BRINKHURST (1971), BRINKHURST (1972) and other works produced by BRINKHURST much attention is focused upon the role of micro-organisms in the diet of tubificids. Different tubificid species can co-exist both vertically and horizontally probably because they feed selectively upon specific micro-organisms. BRINKHURST (1972) has even found mixed tubificid cultures thriving better than pure cultures in laboratory experiments.

Estimations of correlations between different characteristics of the bottom substrate and bottom invertebrates of all kinds have long been of the greatest interest to bottom fauna investigators. There is little need to mention any particular works, but already EKMAN (1915) and ALM (1922) thoroughly discussed such relationships.

Burrowing animals like tubificids and lumbriculids, some chironomid larvae, some amphipods, and copepods are on good grounds supposed to evoke a tremendous effect upon the circulation and irrigation of superficial layers of the sediments. A certain amount of transportation and dislocation of different sediment strata is also most evident, naturally with unknown consequences to palaeobiological investigations (cf. STOCKNER and LUND, 1970).

Under experimental conditions the rate of biochemical oxidation of organic matter in the sediments increased 1.5—2 times in the presence of tubificids according to ZVETKOVA (1972), but SOLOWIEV (1924), RAVERA (1955), KUZNETZOW (1959), SCHUMACHER (1963), WACHS (1967), ZAHNER (1967), and BRINKHURST (1972) also found a strong dependence between the burrowing activities of tubificids in high densities and the circulation of salts, dissolved gases, organic compounds etc. The additional irrigating properties of communities of some chironomid larvae are also of the greatest importance (cf. TESSENOW, 1964; HARGRAVE, 1972; JÓNASSON, 1972).

When macroorganisms are absent, deposits of inorganic mercury in the upper few centimetres of

the sediment are responsible for almost the whole amount of released methyl mercury. If Tubificidae or *Anodonta* are present in high densities, deposits down to 2.5 or 9 cm from the mud surface respectively are effective (JERNELÖV, 1970).

ALSTERBERG (1925) described the active transport of material by tubificid worms in the form of faeces from a depth of feeding of about 2–4 cm in the mud to the surface, but he doubted that tubificids could help ventilating the top sediment layers to any considerable extent. Similar points of view were presented by WAGNER (1968).

Depending upon the season and the actual state of maturity, tubificid worms may be found quite deep in the mud and, according to Russian works, obviously irrespective of where their specific sources of nourishment are concentrated (see above). The obvious vertical separation of adult and juvenile forms of three of the dominating tubificid species in Hovgårdsfjärden are further evidence (see above).

Since all oligochaetes need access to the interface for respiration even normally very deep-burrowing specimens spend much time in the top few centimetres. For that reason it may seem difficult to separate the true vertical preferences from other elementary needs (cf. BRINKHURST *et.al.*, 1969). Naturally, however, there should be better chances of finding the deep-living forms deep in the mud than other worms with less pronounced burrowing habits.

As mentioned before, an adverse relationship between numbers of chironomid larvae (*Chironomus anthracinus*) and tubificids (*Potamothenis hammoniensis*) was observed by JÓNASSON (1972). The same kind of relationship was assumed by BRINKHURST and KENNEDY (1965).

Pontoporeia affinis and larvae of Tanytopodinae and Chironomini are probably the most mobile invertebrates recorded in these investigations.

Big filtrating chironomid larvae like *Chironomus plumosus* are most vulnerable to bottom predating fish like "suckers", but the larvae can stay quite deep in their U-shaped tubes, especially at high oxygen concentrations (cf. BRUNDIN, 1951), thereby reducing their chances of being eaten by fish.

LENZ (1931), BERG (1938), COLE (1953), KAJAK

(1963), BRINKHURST and KENNEDY (1965), and SÄRKKÄ and PAASIVIRTA (1972) have all been aware that some chironomid larvae, *Corethra* larvae or tubificid worms rapidly withdraw into the sediments and congregate at a certain depth if they become aware of a foreign object like a sampler entering the sediments.

The question is now whether this microstratification sampler — which both takes the core and divides it into thin strata in much less than a second — is swift enough to get the big larvae of *Chironomus plumosus*, for instance, at their proper levels of residence in the mud. In any case there is now little doubt that particularly the smallest and most fragile bottom invertebrates are incapable of moving far either vertically or horizontally in the timelapse between the moments when the sampler enters the mud and when it is released.

VI. SUMMARY

The microstratification technique presented here primarily seems to have confirmed some general ideas as to where various bottom invertebrates are dwelling in relation to the mud-water interface.

Naidid oligochaetes were concentrated at the interface, i.e. rarely below a mud depth of 2–4 cm, which is in full agreement with previous works by COLE (1953), STANCZYKOWSKA (1966), SCHIEMER *et.al.* (1969), HOWMILLER and BEETON (1970), SÄRKKÄ and PAASIVIRTA (1972) and BRINKHURST and BRINKHURST *et.al.* (in a series of works) and others. By now it seems quite clear that most naids are more or less bound to the mud surface — or to submerge vegetation (which was not studied here).

On the whole, tubificids penetrated here considerably deeper than naids, even to depths of about 15 cm in the mud, but with maxima of concentration between two and four cm (cf. LENZ, 1931; BERG, 1938; PODOBNAJA, 1961; PODOBNAJA and SOROKIN, 1961; BRINKHURST and KENNEDY, 1965; SOROKIN, 1966; PATARIDZE, 1967; SCHIEMER *et.al.*, 1969; JÓNASSON, 1969, 1972; BRINKHURST *et.al.*, 1969; SÄRKKÄ and PAASIVIRTA, 1972). Some tubificid species like *Limnodrilus hoffmeisteri*, *Potamothenis hammoniensis*, and *Po-*

tamothrix vejdotskyi were with few exceptions, the most deep-penetrating species. *Potamothenis heuscheri* and *Tubifex tubifex* were also capable of penetrating deeply, while *Aulodrilus plurisetus*, in particular, but also *Bothrioneurum vejdotskyanum*, *Aulodrilus pigueti* and some other tubificids displayed as superficial habits as any naidids. The former tubificids are well-known deep-burrowers (cf. SAPKAREV, 1959; PODDUBNAJA, 1961; BRINKHURST and KENNEDY, 1965; JÓNASSON, 1972; SÄRKÄ and PAASIVIRTA, 1972) with the adult worms generally penetrating deepest. These deep migratory movements are not necessarily related to feeding (see discussion). *Aulodrilus plurisetus* often occurs in mud rich in plant fragments (BRINKHURST and JAMIESON, 1971), which makes it more or less bound to the mud surface. The *A. plurisetus* specimens picked out alive from the sediment chambers of the sampler were all, on each occasion, dwelling in tubes of clay lying on the mud surface reminiscent of the tubes of some chironomid larvae.

Bigger specimens of *Chironomus plumosus* were easily distinguishable from other chironomid larvae in that they were dwelling quite deep in the mud (cf. LENZ, 1931; BERG, 1938; BRUNDIN, 1951; JÓNASSON, 1969; SÄRKÄ and PAASIVIRTA, 1972) — often down to 15 cm. It is difficult to say if this is a consequence of repulsive movements by the larvae away from the sampler. Most other chironomid larvae were fairly well concentrated to the upper two centimetres of the mud.

Pontoporeia affinis was generally found a few centimetres below the mud surface, which is also in good agreement with the author's general experience. Ostracoda and Cladocera were located close to the interface, while Copepoda as a rule were the deepest penetrating organisms. Since the bottom material was sorted alive with no preserving additives there should be no confusion concerning dead organisms in the material. In three surveys out of four *Cyclops* spp. had their maxima of occurrence at a depth of about ten centimetres in the sediments. *Cyclops* specimens were quite often found at depths of even about 20 centimetres. Whether they were dormant or not is difficult to say (cf. ELGMORK, 1959), but they were all quite agile when sorted out.

Pisidiids were generally found in the top 2 centimetres of the sediments, but they could also be encountered deeper — at about 10 centimetres (cf. also BERG, 1938, who found them at considerable depths).

VII. REFERENCES

- AAREFJORD, F., R. BORGSTRÖM, L. LIEN, and G. MILBRINK 1973. Oligochaetes in the bottom fauna and in stomach contents of trout, *Salmo trutta* (L.). *Norw. J. Zool.* 21: 281—288.
- ALLEN, K. R. 1942. Comparison of bottom faunas as sources of available fish food. *Trans. Amer. Fish. Soc.* 71: 275—283.
- ALM, G. 1922. Bottenfaunan och fiskens biologi i Yxtasjön — Bottenfauna och fiskavkastning i våra sjöar. *Medd. K. Lantbr.styr. Stockh.* 236. 186 p. (In Swedish with German summary.)
- 1923. Prinzipien der Quantitativen Bodenfaunistik und ihre Bedeutung für die Fischerei. *Verh. int. Ver. Limnol.* 1: 168—180.
- ALSTERBERG, G. 1925. Die Nahrungszirkulation einiger Binnenseetypen. *Arch. Hydrobiol.* 15: 291—338.
- BERG, K. 1938. Studies on the bottom animals of Esrom Lake. *K. Danske Vidensk. Selsk. Skr. Nat. Mat. Afd.* 9, 8: 1—255.
- BORUTSKY, E. V. 1935. Die vertikale Verteilung des Benthos der Bodensedimenteschicht der Seen und ihr Wert als Faktor für die Bewertung des Nährstoffgehaltes der Gewässer. *Tr. Limnol. st. v. Kosine*, (20).
- 1940. Die vertikale Verteilung des Benthos in der abgelagerten Schlammschicht einiger Seen der Moskauer Umgebung. *Zool. Zh.* XIX (2).
- BRINKHURST, R. O. 1969. Changes in the benthos of Lakes Erie and Ontario. *Proc. Conf. Changes in the Biota of Lakes Erie and Ontario. Bull. Buffalo Soc. Nat. Sci.* 25: 45—65.
- 1972. The role of sludge worms in eutrophication. *Project 16010 ECQ U.S. Environmental Protection Agency, Washington, D.C.* 68 p.
- and C. R. KENNEDY 1965. Studies on the biology of the Tubificidae (Annelida, Oligochaeta) in a polluted stream. *J. Anim. Ecol.* 34: 429—443.
- and K. E. CHUA 1969. Preliminary investigation of the exploitation of some potential nutritional resources by three sympatric tubificid oligochaetes. *J. Fish. Res. Bd. Canada* 26(10): 2659—2668.
- K. E. CHUA and E. BATOOSINGH, 1969. Modifications in sampling procedures as applied to studies on the bacteria and tubificid oligochaetes inhabiting aquatic sediments. *J. Fish. Res. Bd. Canada* 26(10): 2581—2593.
- and B. G. JAMIESON 1971. The aquatic Oligochaeta of the world, Oliver and Boyd, Edinburgh, 860 p.

- BRUNDIN, L. 1951. The relation of O₂-microstratification at the mud surface to the ecology of the profundal bottom fauna. *Rep. Inst. Freshw. Res. Drottningholm* 32: 32—43.
- COLE, G. A. 1953. Notes on the vertical distribution of organisms in the profundal sediments of Douglas Lake, Michigan. *Amer. Midl. Nat.* 49(1): 252—256.
- DEKSBACH, N. K. 1939. Die vertikale Verteilung des Benthos in der Schlamm-schichtablagerung in den Gewässern der Umgebung Moskaus. *Bjull. Mosk. obšč. isp. prirody, otd. biol.* 48 (4).
- DIGERFELDT, G. and U. LETTEVALL 1969. A new type of sediment sampler. *Geol. Fören. Stockh. Förh.* 91: 399—406.
- EDMONDSON, W. T. and G. G. WINBERG. Eds., 1971. A manual on methods for the assessment of secondary productivity in fresh waters. IBP Handbook 17, 358 p.
- EFFORD, I. E. 1960. A method for studying the vertical distribution of the bottom fauna in shallow waters. *Hydrobiologia* 16(3): 288—292.
- EKMAN, S. 1915. Die Bodenfauna des Vättern qualitativ und quantitativ untersucht. *Int. Rev. Hydrobiol.* 7(2/3): 146—205, 275—426.
- ELGMORK, K. 1959. Seasonal occurrence of *Cyclops strenuus* in relation to environment in small water bodies in southern Norway. *Folia limnol. scand.* 11: 1—196.
- 1962. A bottom sampler for soft mud. *Hydrobiologia* 20(2): 167—172.
- FAGER, E. W. 1966. Equipment for use in ecological studies using SCUBA. *Limnol. & Oceanogr.* 11(4): 503—509.
- FORD, J. B. 1962. The vertical distribution of larval Chironomidae (Dipt.) in the mud of a stream. *Hydrobiologia* 19(3): 262—272.
- GALINSKY, V. L. and V. F. NIKITIN 1972. On the method of calculation of the Oligochaeta in the fish's intestines. The aquatic Oligochaeta. *Trans. Hydrobiol. Soc. USSR*, XVII 167—176.
- GRIGELIS, A. I. 1966. Biochemical evaluation of different oligochaetes in a series of running waters in the Lithuanian USSR. *Rep. Lithuanian Acad. Sci. Vilna. Ser. V*, 1(39). (In Russian).
- GRIMÅS, U. 1963. Reflections on the availability and utilization degree of bottom animals as fish food. *Zool. Bidr. Uppsala* 35: 497—503.
- HARGRAVE, B. T. 1972. Oxidation-reduction potentials, oxygen concentration and oxygen uptake of profundal sediments in Lake Esrom. *Oikos* 23: 166—177.
- HAYNE, D. W. and R. G. BALL, 1956. Benthic productivity as influenced by fish predation. *Limnol. & Oceanogr.* 1(3): 162—175.
- HOPKINS, T. L. 1964. A survey of marine bottom samplers. In: *Progress in Oceanography*, 2. Pergamon Press. 41 p.
- HOWMILLER, R. P. and A. M. BEETON 1970. The oligochaete fauna of Green Bay, Lake Michigan. *Proc. 13th Conf. Great Lakes Res.* 1970: 15—46.
- JERNELÖV, A. 1970. Release of methyl mercury from sediments with layers containing inorganic mercury at different depths. *Limnol. & Oceanogr.* 15(6): 958—960.
- JÓNASSON, P. M. 1969. Bottom fauna and eutrophication. p. 274—305. In: *Eutrophication: Causes, Consequences, Correctives*, N.A.S. Washington D.C.
- 1972. Ecology and production of the profundal benthos. *Oikos, suppl.* 14. 148 p.
- KAJAK, Z. 1963. Analysis of quantitative benthic methods. *Ekol. Polsk A*, 11(1): 1—56.
- KENNEDY, C. R. 1969. Tubificid oligochaetes as food of dace *Leuciscus leuciscus* (L.). *J. Fish. Biol.* 1(1): 11—15.
- and P. J. WALKER. 1969. Evidence for an immune response by dace, *Leuciscus leuciscus*, to infections by the cestode *Caryophyllaeus laticeps*. *J. Parasit.* 55: 579—582.
- KIRPICENKO, M. JA. 1940. Die benthale Fauna der Marschgewässer des Dnjeperbeckens bei Zigansk und Podborno. *Tr. Kievskoj gidrobiol. st AN SSSR* 1(4).
- KJÄLLMAN, A. and U. GRIMÅS 1967. Lilla Ullevifjärden. Bottenfaunan. *Zool. Rev. Stockh.* 1: 30—33.
- KUZNETZOV, S. I. 1959. Die Rolle der Mikroorganismen im Stoffkreislauf der Seen. Berlin. 301 p.
- LENZ, F. 1931. Untersuchungen über die Verteilung der Bodenfauna im Tiefsediment von Seen. Ein neuer Bodengeifer mit Zerteilungsvorrichtung. *Verb. int. Ver. Limnol.* 5: 232—260.
- MILBRINK, G. 1968. A Microstratification sampler for mud and water. *Oikos* 19(1): 105—110.
- 1969. Microgradients at the mud-water interface. *Rep. Inst. Freshw. Res. Drottningholm* 49: 129—148.
- 1971. A simplified tube bottom sampler. *Oikos* 22: 260—263.
- 1972. On the horizontal distribution of the profundal bottom fauna in a limited area of central Lake Mälaren, Sweden. In: PhD-thesis, Uppsala. 22 p.
- 1973. On the use of indicator communities of Tubificidae and some Lumbriculidae in the assessment of water pollution in Swedish lakes. *ZOON* 1: 125—139.
- MORTIMER, C. H. 1941/1942. The exchange of dissolved substances between mud and water in lakes. *J. Ecol.* 29: 280—329, 30: 147—201.
- MUUS, B. J. 1967. The fauna of Danish estuaries and Lagoons. Distribution and ecology of dominating species in the shallow reaches of the Mesohaline Zone. *Medd. Danm. Fisk. Havunders. N.S.* 5(1). 316 p.
- NAUMANN, E. 1930. Einführung in die Bodenkunde der Seen. *Binnengewässer* 9. 126 p.
- PATARIDZE, A. I. 1967. On the vertical distribution of oligochaetes in the sediment strata of the Tiflis impoundment. Materials of the 1st All-Union Symposium on the Aquatic Oligochaeta in Tartu, 1967. p. 23—25. (Translated from Russian.)

- PODDUBNAJA, T. L. 1961. Über die vertikale Verteilung der *Limnodrilus newaensis* MICH. und *L. hoffmeisteri* CLAP. in der Schlammsschicht des Rybinsker Stausees. *Byull. Inst. Biol. Vodochr.* 12: 20—26.
- 1962. Consumption of Tubificidae by fish. *Probl. Ichthyology* 2(3): 560—562.
- and J. I. SOROKIN 1961. The thickness of the nutrient layer in connection with the movements of the Tubificidae in the ground. *Byull. Inst. Biol. Vodochr.* 10: 14—17.
- POPCHENKO, V. I. 1971. Consumption of Oligochaeta by fishes and invertebrates. *J. Ichthyology* 11(1): 75—80.
- RAVERA, O. 1955. Amount of mud displaced by some freshwater oligochaeta in relation to the depth. *Mem. Ist. Ital. Idrobiol., Suppl.* 8: 247—264.
- RICKER, W. E. 1952. The Benthos of Cultus Lake. *J. Fish. Res. Bd. Canada* 9(4): 204—212.
- SAPKAREV, J. 1959. *Ilyodrilus hammoniensis* MICH. (Oligochaeta) in the large lakes of Macedonia (Ohrid, Prespa, and Dojran). *Rev. Trav. Sta. Hydrobiol. Obria.* 7 1459, 1.
- SCHIEMER, F., H. LÖFFLER, and H. DOLLFUSS 1969. The benthic communities of Neusiedlersee (Austria). *Verh. int. Ver. Limnol.* 17: 201—208.
- SCHUMACHER, A. 1963. Quantitative Aspekte der Beziehung zwischen Stärke der Tubificidenbesiedlung und Schichtdicke der Oxydationszone in den Süßwasser der Unterelbe. *Arch. FischWiss.* 14(1/2): 48—50.
- SOLOWIEV, M. M. 1924. Über die Rolle der *Tubifex tubifex* in der Schlammerzeugung. *Int. Rev. Hydrobiol.* 12(1/2): 90—101.
- SOROKIN, J. I. 1966. Carbon-14 Method in the study of the nutrition of aquatic animals. *Int. Rev. Hydrobiol.* 51(2): 209—224.
- SPERBER, C. 1948. A taxonomical study of the Naididae. *Zool. Bidr. Uppsala* 28. 296 p.
- STAŃCZYKOWSKA, A. 1966. Some methodical problems in zoomicrobenthos studies. *Ekol. Polsk, A*, 14(23): 385—393.
- STOCKNER, J. G. and J. W. G. LUND. 1970. Live algae in postglacial deposits. *Limnol. & Oceanogr.* 15(1): 41—58.
- SÄRKKÄ, J. and L. PAASIVIRTA 1972. Vertical distribution and abundance of the macro- and meiofauna in the profundal sediments of Lake Päijänne, Finland. *Ann. Zool. Fennici* 9(1): 1—9.
- TESSENOW, U. 1964. Experimentaluntersuchungen zur Kieselsäurerückführung aus dem Schlamm der Seen durch Chironomidenlarven (Plumosus-Gruppe). *Arch. Hydrobiol.* 60(4): 497—504.
- WACHS, B. 1967. Die Oligochaeten-Fauna der Fließgewässer unter besonderer Berücksichtigung der Beziehungen zwischen der Tubificiden-Besiedlung und dem Substrat. *Arch. Hydrobiol.* 63(3): 310—386.
- WAGNER, G. 1968. Zur Beziehung zwischen der Besiedlungsdichte von Tubificiden und dem Nahrungsangebot im Sediment. *Int. Rev. Hydrobiol.* 53(5): 715—721.
- WAVRE, M. and R. O. BRINKHURST 1971. Interactions between some tubificid Oligochaetes and bacteria found in the sediments of Toronto Harbour, Ontario. *J. Fish. Res. Bd. Canada* 28(3): 335—341.
- YAROSHENKO, M., O. VALKOVSKAYA, and V. CHOKIRLAN 1972. The aquatic Oligochaeta and their significance as food of fishes. The aquatic Oligochaeta, *Trans. Hydrobiol. Soc. USSR* XVII: 162—167.
- ZAHNER, R. 1967. Experimente zur Analyse biologischer, chemischer und physikalischer Vorgänge in der Wasser-Sediment-Grenzschicht stehender und langsam strömender Gewässer. *Int. Rev. Hydrobiol.* 52(4): 627—645.
- ZVETKOVA, L. J. 1972. Oligochaeta in the oxygen balance of reservoirs. The aquatic Oligochaeta. *Trans. Hydrobiol. Soc. USSR* XVII: 118—125.

On the Relation Between Fish Fauna and Zooplankton Composition in North Swedish Lakes

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I. INTRODUCTION

Interaction between fish species has been one of the favourite topics of Swedish fishery biology since the 1950s. The relatively simple ecosystems of the North Scandinavian lakes, containing only one, two or three species of fish or even being empty of fish, have provided excellent possibilities of comparing allopatric populations of fish with sympatric ones, as well as studying the effect of introducing new species. A common sequence as regards the late history of the Scandinavian mountain lakes has been: (1) introductions of either brown trout or char into barren lakes, (2) addition of a new species (trout or char) to produce a two-species system, and finally (3) addition of a third species or even further ones, e.g. whitefish, burbot and pike.

As regards the interaction between brown trout (*Salmo trutta* L.) and arctic char (*Salvelinus alpinus* L.), early Norwegian experiences showed the existence of food competition (cf. DAHL 1920). Studies in Swedish lakes indicated that it was benthic animals, above all *Gammarus lacustris* SARS, for which the two species competed, the ultimate result being a decreased growth rate and an "interactive segregation" of the fish species (NILSSON 1965, 1967). Similar phenomena were observed in different coexisting species of *Coregonus* (SVÄRDSON 1954, NILSSON 1960, LINDSTRÖM and NILSSON 1962). Whitefish introduced into lakes containing arctic char often eliminated the char populations (EKMAN 1910), and SVÄRDSON (1961) listed 14 lakes where arctic char had disappeared or had markedly decreased after the introduction of whitefish. He speculated that either the big whitefish were feeding on the newly hatched char fry or the elimination of char was a result of severe food competition among the young as well as the adult fish.

The evidence brought together by BROOKS, DODSON, GALBRAITH, SMITH, WELLS and others that the grazing of fish can alter the composition of the plankton fauna even in rather large bodies of water, together with the fact that arctic char introduced into a barren lake could eliminate the planktic crustacean *Poyartemia forcipata* (KARLSSON and NILSSON 1968, NILSSON 1972a), prompted the present regional investigation aimed at finding out whether there exists a correlation between the fish fauna and the zooplankton composition in North Swedish lakes.

II. MATERIAL AND METHODS

As the investigation aimed at ascertaining whether there are species of planktic crustaceans that are affected by fish predation, we have grouped the surveyed lakes according to their fish fauna. There are, of course, many other parameters to be taken into consideration. For instance, the elevation above sea level ranges from 1,325 metres (Kuoblatjåkkjojaure) to less than 300 metres. The lakes vary in size from 160 km² (Storuman) to less than 2 km². They are, however, all (except Övre Heimdalsvann) situated in the North Swedish forest or mountain region from the Ljusnan river system in south (about 62°N) to the Torne river system (about 68°N), and many of the "type" lakes with different fish faunas are connected to each other by brooks and rivers (cf. Table 1 and maps, Figs. 1—3). It may further be observed that some of the lakes categorized as char-trout lakes further contain, for example, grayling and/or burbot, and the lakes categorized as whitefish lakes often contain brown trout, pike and perch as well.

Table 1. *List of lakes investigated (including those of cited previous publications), catalogued according to composition of fish fauna and river systems.*

- I. *Fishless lakes*
- River Torneälven:
1. Kuoblatjåkkojaure
 2. Latnjaure
 3. Rissaure
 4. Råtjoaure
 5. Tjåmohasjaure
- River Kalixälven:
1. Tarfalsjön
- River Luleälven:
1. Rovejaure 15
 2. Rovejaure 17
- River Piteälven:
1. Rovejaure II: 1
 2. Puojtes A
 3. Puojtes B
- II. *Trout-lakes*
- River Torneälven:
1. Katterjaure
- River Luleälven:
1. Tåresjaure
 2. Parkajaure
- River Umeälven:
1. Ropen
 2. Arevattnet
 3. Abelvattnet
- River Ångermanälven:
1. Vårgaren
 2. Lejaren
 3. Oratjaure
- River Glåma (Norway):
1. Övre Heimdalsvann
- III. *Char-lakes*
- River Torneälven:
1. Abiskojaure
 2. Vuolep Allesjaure
- River Luleälven:
1. Aronjaure
- River Vapsälven:
1. Skalvattnet
- River Ångermanälven:
1. Dårestjärn
- IV. *Char-trout-lakes*
- River Umeälven:
1. Överuman
 2. Tärnasjön
3. Tångvattnet
 4. Jovattnet
 5. Övre Björkvattnet (before 1963)
- River Ångermanälven:
1. Ransaren
 2. Kultsjön
 3. Borgsjön
 4. Storsjouten
 5. Stora Blåsjön
 6. Jormsjön
 7. Kvarnbergsvattnet
- River Indalsälven:
1. Stora Mjölkvattnet
 2. Torrön
 3. Ottsjön
 4. Håckren
 5. Rengen
 6. Gesten
 7. Gevsjön
 8. Ännsjön
 9. Hottön
- River Ljusnan:
1. Övre Grundsjön
 2. Nedre Grundsjön
 3. Mässlingen
- V. *Char-trout-whitefish-lakes*
- River Torneälven:
1. Torneträsk
- River Umeälven:
1. Gardiken
 2. Övre Björkvattnet (after 1963)
 3. Storuman
- River Ångermanälven:
1. Ströms Vattudal
- VI. *Whitefish-lakes*
- River Torneälven:
1. Nedre Laksjön
 2. Luossajärvi
 3. Rakkurijärvi
- River Umeälven:
1. Västansjön
 2. Fjosokken
 3. Storjuktan
- River Ångermanälven:
1. Vojmsjön
- River Indalsälven:
1. Sällsjön
- River Ljusnan:
1. Övre Särvsjön
 2. Nedre Särvsjön

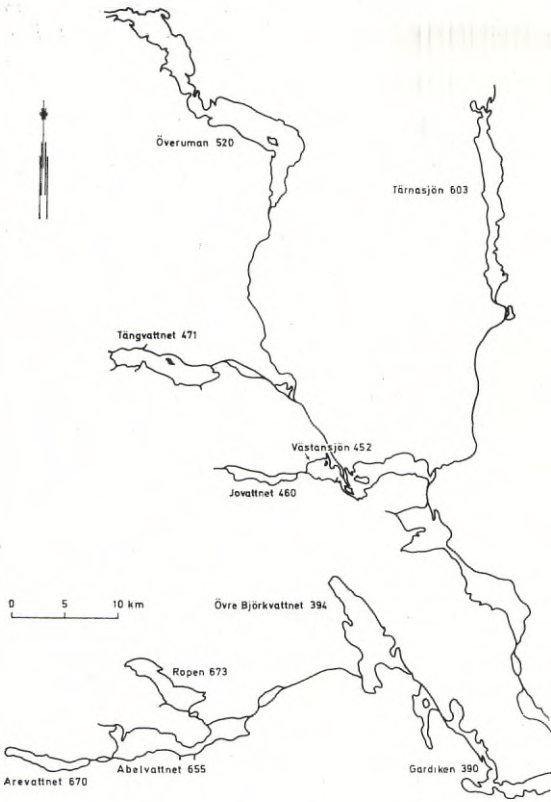


Fig. 1. Map showing the investigated lakes of the Umeälven river system.

The samples collected by ourselves (presented in Table 1) were taken with a plankton net (dimension 75 μ). Hauls were taken in a standardized way, *i.e.* by vertical hauling preferably over the largest depth of the lake, the net being drawn back and forth five times to a certain depth. As we are aware that this method gives no basis for quantitative calculations, we have only expressed differences in the occurrence of the different species in the samples as subjective records realized as frequency signs (Table 2).

The measurements (Figs 4—9) are based exclusively upon sexually mature animals: in the case of the cladocerans only females are included, in that of the copepods both males and females. The mode of measurement is in accordance with BROOKS 1968, *i.e.* the caudal spine (in *Daphnia* and *Bosmina*), antennae and caudal setae (in the copepods) are excluded, while the helmet some-

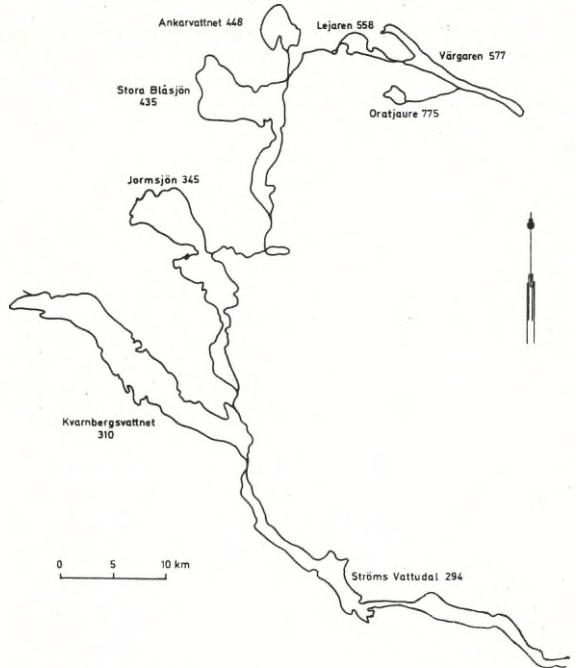


Fig. 2. Part of the lake system of the Faxälven river (an affluent of the Ångermanälven river).

times occurring in *Daphnia* is included. If available, 50 specimens from each population were measured (in the case of the copepods 50 of each sex).

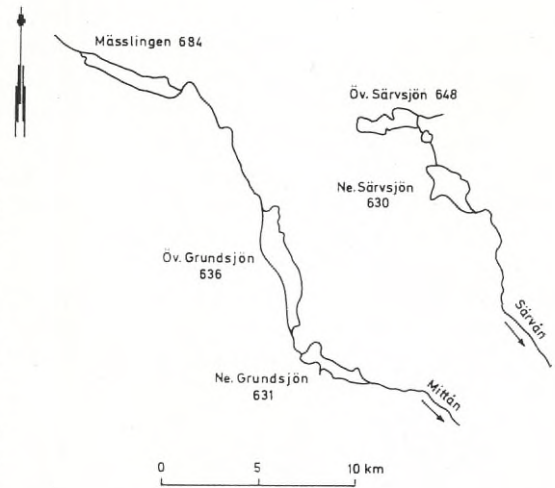


Fig. 3. The investigated lakes of the Ljusnan river.

Table 2. Composition of crustacean zooplankton in the samples studied by the present authors. As no species in the sample, but the total amount of plankton, collected in unit time, has also been taken into

	1. Fishless lakes								
	Rovejaure 15	Rovejaure 17	Rovejaure II: 1	Puojtes A	Puojtes B	Tåresjaure	Parkajaure	Ropen	Arevattnet
	8. VIII 1968	8. VIII 1968	8. VIII 1968	12. VIII 1968	13. VIII 1968	19. VIII 1968	20. VIII 1968	30. IX 1970	5. VIII 1960
<i>Polyartemia forcipata</i>	-	-	-	-	-	+++	-	-	-
<i>Holopedium gibberum</i>	-	-	-	-	+	++	-	++	-
<i>Daphnia longispina</i> s.str.	+++	+	-	++	+++	-	-	++	+
<i>Daphnia galeata</i>	-	-	-	-	-	-	+++	-	-
<i>Daphnia cristata</i>	-	-	-	-	-	-	-	-	-
<i>Ceriodaphnia quadrangula</i>	-	-	-	-	-	-	-	-	-
<i>Bosmina coregoni</i>	-	-	+++	++	++	++	++	++	++
<i>Bosmina longirostris</i>	-	-	-	-	-	-	-	-	-
<i>Bythotrephes longimanus</i>	-	-	-	-	-	-	-	-	++
<i>Heterocope saliens</i>	-	-	-	-	-	-	-	+	-
<i>Heterocope appendiculata</i>	-	-	-	-	-	-	-	-	-
<i>Eudiaptomus graciloides</i>	-	-	-	-	-	-	-	-	-
<i>Acanthodiptomus denticornis</i>	-	-	-	-	-	-	-	-	-
<i>Arctodiptomus laticeps</i>	+	++	++	-	-	-	-	++	++
<i>Mixodiptomus laciniatus</i>	-	-	-	-	-	-	-	-	-
Diaptomidae sp.	-	-	-	+	++	-	-	-	-
Cyclopidae sp.	++	+++	+++	++	+++	+	++	+++	-

In order to increase the material to be discussed, we also include previous publications, where these refer to plankton samples collected in the central parts of the lakes and comprising not only the surface layer and where, in addition, reliable data on fish fauna were available. Thus the following papers are considered in Table 3: LINDSTRÖM (1951, 1958) for Lakes Ottsjön, Håckren, Gesten, Ånnsjön (=Ånn), Hottön and Sällsjön; LÖFFLER (1953) for Lakes Stora Blåsjön (=Blåsjön), Jormsjön, Kvarnbergsvattnet and Ströms Vattudal (=the following localities mentioned in LÖFFLER's paper: Torsfjärden, Gärdnäs-Hillsand, Äspnäs, Ösjön and Russfjärden); AXELSON (1961) for Lakes Ransaren and Kultsjön; LÖTMARKER (1964) for Lakes Överuman, Övre Björkvattnet, Borgasjön, Storsjouten, Stora Mjölkvattnet, Torrön, Ottsjön, Rengen, Storuman, Fjosokken, Storjuktan and Vojmsjön; NAUWERCK (1967) for Lake Latnjajaure; HOLMGREN (1968) for Lake Nedre Laksjön; BRELIN and JÓHANNSSON

(in the press) for Lake Stora Blåsjön. The waters from Torsfjärden onwards, down to Russfjärden (see above), are in the main considered as one continuous lake called Ströms Vattudal, and are so designated in our Table 2. The samples from Lake Övre Björkvattnet collected before 1963 are reported by LÖTMARKER (*op.cit.*), while those collected after 1963 were studied by the present authors.

From the late Professor SVEN EKMAN's annotations we have collected the data concerning the following lakes in northern Lapland: Kuoblatjåkkajaure, Rissajaure, Råtjojaure, Tjåmohasjaure, Tarfalasjön, Katterjaure, Abiskojaure, Vuolep Allesjaure, Torneträsk, Luossajärvi and Rakkurijärvi. As in many cases only genus names were written in these annotations, species determinations had to be carried out by ourselves, utilizing EKMAN's preserved material. For a description of these lakes the reader is referred to EKMAN (1957) and, for a comparison of EKMAN's older and more

quantitative samples were taken, frequency signs, +, ++ and +++ mainly express density in relation to the other consideration.

				2. Trout-lakes								3. Char-lakes						
Abelvattnet				Värgaren				Lejaren				Oratjaure	Aronjaure	Skalvattnet				Dårestjärn
2. VIII 1960	19. VIII 1960	27. VIII 1970	30. IX 1970	9. VIII 1967	8. VIII 1968	2. VIII 1970	14. VIII 1971	5. VIII 1969	5. VIII 1970	10. VIII 1971	30. VII 1970	24. VII 1968	13. VII 1960	25. VII 1960	8. VIII 1960	22. VIII 1960	30. VII 1970	
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
++	++	++	++	+++	+	+++	+++	+	+++	+++	+	+++	++	+++	+++	+++	+	-
+	++	+	++	+	++	++	+	++	++	+++	-	-	-	-	+	-	-	-
+	++	-	++	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
++	++	+	++	++	+++	++	+++	+++	++	+	+	+++	++	+++	+++	+++	+++	+++
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	+	-	-	-	-	+	-	-	+	+	-	-	-	-	-	-	-	-
-	+	++	+	+++	+++	++	++	++	++	++	++	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
++	+++	++	++	++	+	++	+++	+++	++	+++	-	-	+	++	++	++	++	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+++
-	-	-	-	-	-	-	-	-	-	-	+++	-	-	-	-	-	-	-
+++	+++	-	+++	++	+	++	+++	+++	++	+++	-	+++	+++	+++	+++	+++	+++	+

recent data, to HJELM (1972). Finally, for the data concerning Lake Övre Heimdalsvann in the Jotunheimen area (Norway) we are indebted to the Norwegian zoologist PETER LARSSON.

In the tables as well as in the discussion only purely planktic species are considered. Thus, e.g., *Sida crystallina* (MÜLL.) and *Polyphemus pediculus* L. are excluded, as they belong mainly to the littoral zone and occur only sporadically in plankton samples from the central parts of the lakes. The inclusion of *Polyartemia forcipata* among the plankters may seem surprising, but this species did in fact occur as a purely pelagic animal in Lake Tåresjaure, as it also did in Lake Pieskejaure (NILSSON 1972a) and Lake Övre Laksjön (unpublished observations by B. PEJLER). The reason for this seemingly deviant behaviour is discussed below, at p. 66.

The form treated by LÖTMARKER (*op.cit.*) as "*Daphnia cristata* subsp. *longiremis* Sars" was originally considered by Sars as well as by

BROOKS (1957) to be a species of its own, and this view is adopted in Table 3. As LÖTMARKER found only a few individuals, and these almost exclusively from the hypolimnion, this species will not be mentioned in the discussion.

In the case of *Cyclopidae*, mostly only nauplii and copepodids were found, as our samples were mainly collected during one season only, viz. late summer and autumn. In most cases where adult males and females occurred, they appeared to belong to *Cyclops scutifer* Sars, and this species was observed in several lakes treated in the cited papers and also by the present authors in Lakes Rovejaure 15, Rovejaure 17, Rovejaure II: 1, Puojtes A, Puojtes B, Parkajaure, Abelvattnet, Värgaren, Lejaren, Aronjaure, Skalvattnet, Dårestjärn and Övre Björkvattnet. In some cases the diaptomids, too, were represented only by immature individuals, and this is the reason for the designation "*Diaptomidae* sp." used for some of the samples.

Table 2 continued.

	4. Char-trout-lakes						
	Tärnasjön	Tångvattnet	Jovattnet	Övre Grundsjön	Nedre Grundsjön	Mässlingen	
	30. VII 1970	31 IX 1970	23. VII 1970	29. IX 1970	17. IX 1970	17. IX 1970	16. IX 1970
<i>Polyartemia forcipata</i>	-	-	-	-	-	-	-
<i>Holopedium gibberum</i>	-	+++	+	-	++	+	-
<i>Daphnia longispina</i> s.str.	-	-	-	-	-	-	-
<i>Daphnia galeata</i>	+++	++	++	++	+	++	+
<i>Daphnia cristata</i>	-	-	-	-	-	-	-
<i>Ceriodaphnia quadrangula</i>	-	-	-	-	-	-	-
<i>Bosmina coregoni</i>	++	+++	+++	++	+	+++	++
<i>Bosmina longirostris</i>	-	-	-	-	-	-	-
<i>Bythotrephes longimanus</i>	-	-	-	-	-	-	-
<i>Heterocope saliens</i>	++	-	+	-	-	-	-
<i>Heterocope appendiculata</i>	-	-	-	-	-	-	-
<i>Eudiaptomus graciloides</i>	++	+++	-	+++	-	-	-
<i>Acanthodiaptomus denticornis</i>	-	-	-	-	-	-	-
<i>Arctodiaptomus laticeps</i>	-	+	-	-	+	-	+
<i>Mixodiaptomus laciniatus</i>	-	-	-	-	-	-	-
Diaptomidae sp.	-	-	+++	-	-	-	-
Cyclopidae sp.	++	+++	+	+	++	++	+++

Concerning the taxonomy of the *Daphnia* forms encountered, the reader is referred to PEJLER (1973). It was not possible for us to apply the taxonomy proposed by LIEDER (1957) for the genus *Bosmina*, mainly based upon Central European material, and we therefore had to rely upon older literature such as BURCKHARDT (1941). As regards the other cladocerans the nomenclature used by HERBST (1962) is followed. The taxonomy of the copepods is hardly controversial, the determination of species being made mainly with the aid of SARS 1903 and KIEFER 1960. For the complete names of the species the reader is referred to Table 3.

III. OCCURRENCE OF THE PLANKTIC CRUSTACEANS

Results

From the exposition on p. 55 it is evident that *C. scutifer* occurs in all the categories of lakes

quoted on the basis of their fish fauna. *Bosmina coregoni* s.l. is another species (or species group?) exhibiting this wide amplitude and occurring in most lakes (Tables 2—3). More restricted in occurrence but found in at least one lake of each category are *Holopedium gibberum* and *Arctodiaptomus laticeps*. *Daphnia galeata* and *Bythotrephes longimanus* were encountered in all types of lakes except the fishless ones, while *Eudiaptomus graciloides* was missing only in the category "trout lakes".

Some species were found so sporadically that no conclusions can be drawn in this connection. The distribution of the following species, however, merits special attention. *Daphnia longispina* s.str. (for definition see PEJLER, 1973) was found only in fishless lakes and trout lakes, but in a great many of these (and also in two lakes with recently introduced char which on the occasion of sampling occurred in such a low number that it could hardly have had a noticeable effect on zooplankton composition). *D. cristata*, on the other

Table 2 continued.

5. Char-trout-whitefish-lakes									6. Whitefish-lakes					
Gårdiken	Övre Björkvattnet (after 1963)								Nedre Laksjön	Västansjön	Övre Särvsjön	Nedre Särvsjön		
30. VII 1970	17. VIII 1965	24. VIII 1965	8. IX 1965	9. X 1967	11. IX 1968	23. IX 1968	18. IX 1969	23. VII 1970	25. IX 1967	17. VII 1970	23. VII 1970	29. IX 1970	16. IX 1970	16. IX 1970
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
+	+	+	++	+	+	-	+	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
+	+++	++	+++	+++	+++	+	++	+	+	+	++	++	-	+
-	-	-	-	-	-	-	-	-	-	-	-	-	++	++
+	-	-	-	-	-	-	-	-	-	++	-	-	-	++
+	++	+	++	+++	+++	+++	++	++	++	++	+	++	++	+++
-	-	-	-	-	-	-	-	-	-	-	+++	-	++	+
-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
+	+	-	+	+	++	+	+	-	-	-	-	-	-	-
+++	++	+++	+	+++	+++	+++	+	-	+++	+++	++	-	-	-
-	-	-	-	-	-	-	-	-	-	-	++	++	-	+
+	+++	+++	++	-	++	-	-	++	-	-	-	-	-	+
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
+++	+	+	++	+++	++	+	+	+++	+++	++	++	++	++	++

hand, was encountered in 9 of the lakes containing whitefish and in one of the char-trout lakes, but not in any of the many lakes of categories 1—3 investigated. A confinement of *D. cristata* to whitefish lakes is also reported by LÖTMARKER (*op.cit.*, p. 162 and 169), though he gives a different explanation for this from the one given below. Furthermore, LANGELAND (1972), comparing his Norwegian material with that of HUITFELDT-KAAS (1906), reports that *D. cristata* was not found in Lake Nevelvatn before the introduction of whitefish, but occurred in great masses after that introduction.

Returning to our own material, *Ceriodaphnia quadrangula* and *Bosmina longirostris* were collected only from lakes inhabited by whitefish.

Heterocope saliens was found in 6 trout lakes and in 17 char-trout lakes, but in only one of the many lakes with whitefish populations. The only exception, Lake Ströms Vattudal, is part of a lake chain and is separated by a waterfall from the

next lake upstream (see LÖFFLER, *op.cit.* p. 60 and 63). This waterfall acts as a barrier against the whitefish, which are therefore confined to the parts below it. However, a continuous afflux of zooplankton in the opposite direction can be presumed to occur, and it may therefore be surmised that the specimens of *H. saliens* found in Lake Ströms Vattudal are mainly introduced from the parts situated upstream, especially as they occurred scattered (> 1 per cent) in the samples and chiefly in the upper part of the reservoir.

H. appendiculata, on the other hand, appeared in the samples from 8 lakes containing whitefish but not in any of the first four categories. Especially striking are the conditions in Lake Övre Björkvattnet, from which LÖTMARKER (1964) reports only *H. saliens*. After LÖTMARKER's investigation, whitefish immigrated into the lake as a result of the damming of a lake situated below. Our samples, taken three years or more after the immigration, appeared to contain *H. appendicu-*

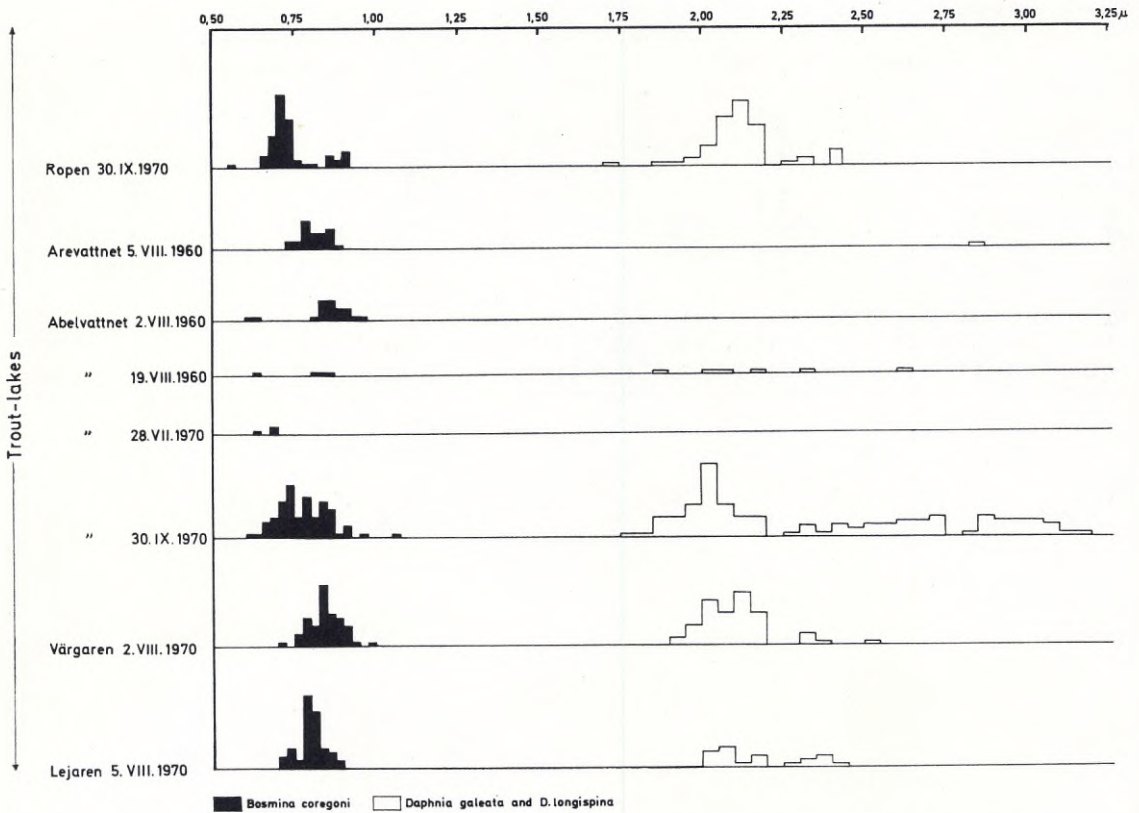


Fig. 4. Body length (for definition and mode of measurement, see p. 53) of mature females of the genera

Bosmina and *Daphnia* in certain trout lakes.

lata in great numbers but no *H. saliens* at all. In the case of the chain of lakes studied by LÖFFLER, *H. appendiculata* was found only in Lake Ströms Vattudal, i.e. below the barrier-forming waterfall mentioned above.

The possibility that some other factor, coincident with fish distribution, (e.g. length of the ice-free season) is responsible for the mentioned correlations, seems extremely slight, as there is a wide variation concerning abiotic factors within each of the lake categories, the composition of fish fauna being the product as much of historical reasons (immigration, transplantation) as of current environmental conditions. In addition to the above-mentioned replacement of *Heterocope saliens* by *H. appendiculata* in Övre Björkvattnet the facts mentioned in the following three paragraphs should be taken into account.

The whitefish lakes Övre Särvsjön and Nedre Särvsjön are situated in the same area as the char-trout lakes Övre Grundsjön, Nedre Grundsjön and Mässlingen. The environmental conditions for all these lakes are very similar, as regards geological foundation, height above sea level, size order of area and depth, ice-free season, etc. In spite of this, there is a striking difference between the two groups as regards zooplankton composition. Above all, it may be mentioned that three of the species, reported above as characteristic of whitefish lakes (viz. *Daphnia cristata*, *Ceriodaphnia quadrangula* and *Bosmina longirostris*), are found in the Särvsjön lakes but are missing in the samples from the char-trout lakes (cf. also NILSSON 1972b).

In the same way we may compare Lakes Jovattnet and Västansjön, the former being a char-

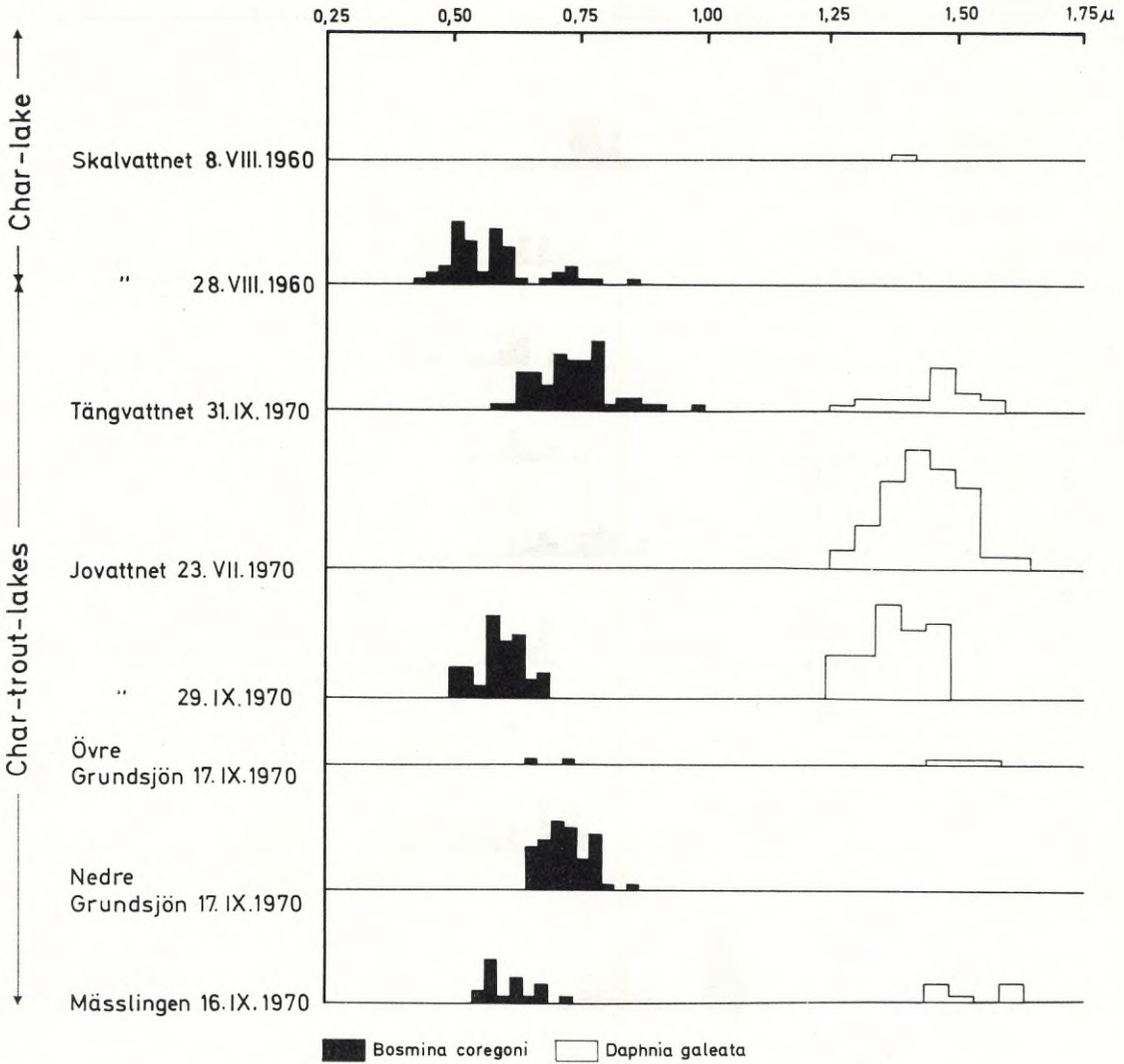


Fig. 5. Body length of *Bosmina* and *Daphnia* in a char lake and certain char-trout lakes.

trout lake, the latter a whitefish lake. Though they lie close together in the same river system, are situated at almost the same altitude (460 and 452 m above sea level, respectively) and show roughly the same general characteristics, their zooplankton differs remarkably, e.g. *Heterocope saliens* being found in Lake Jovattnet and *Bosmina longirostris* sometimes dominating in Lake Västan-sjön.

The lake system of the River Faxälven (an affluent of the River Ängermanälven) affords

similar examples: Its lower parts (Ströms Vattudal) were discussed above concerning *Heterocope appendiculata*. In each of the six lakes above the waterfall referred to which are included in Table 2, *H. saliens* was found but not *H. appendiculata*. The three uppermost lakes (Oratjaur, Värgaren, Lejaren) contained trout as the only fish, and in two of them the "exclusive" *Daphnia longispina* s.str. was found in great numbers. On the other hand, this species was not encountered in the char-trout lakes situated downstream, e.g. not in the

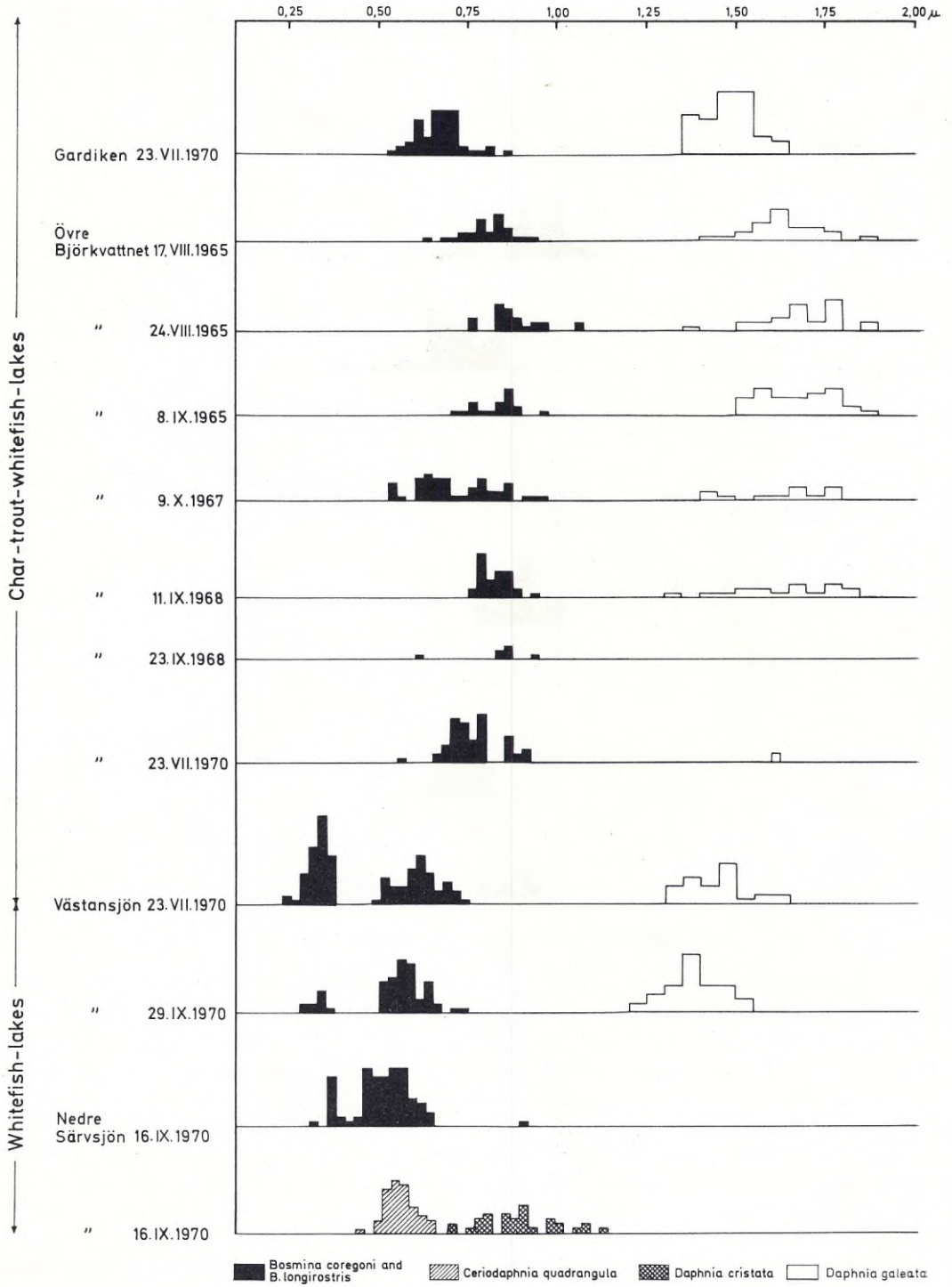


Fig. 6. Body length of the dominant cladocerans in certin lakes containing whitefish.

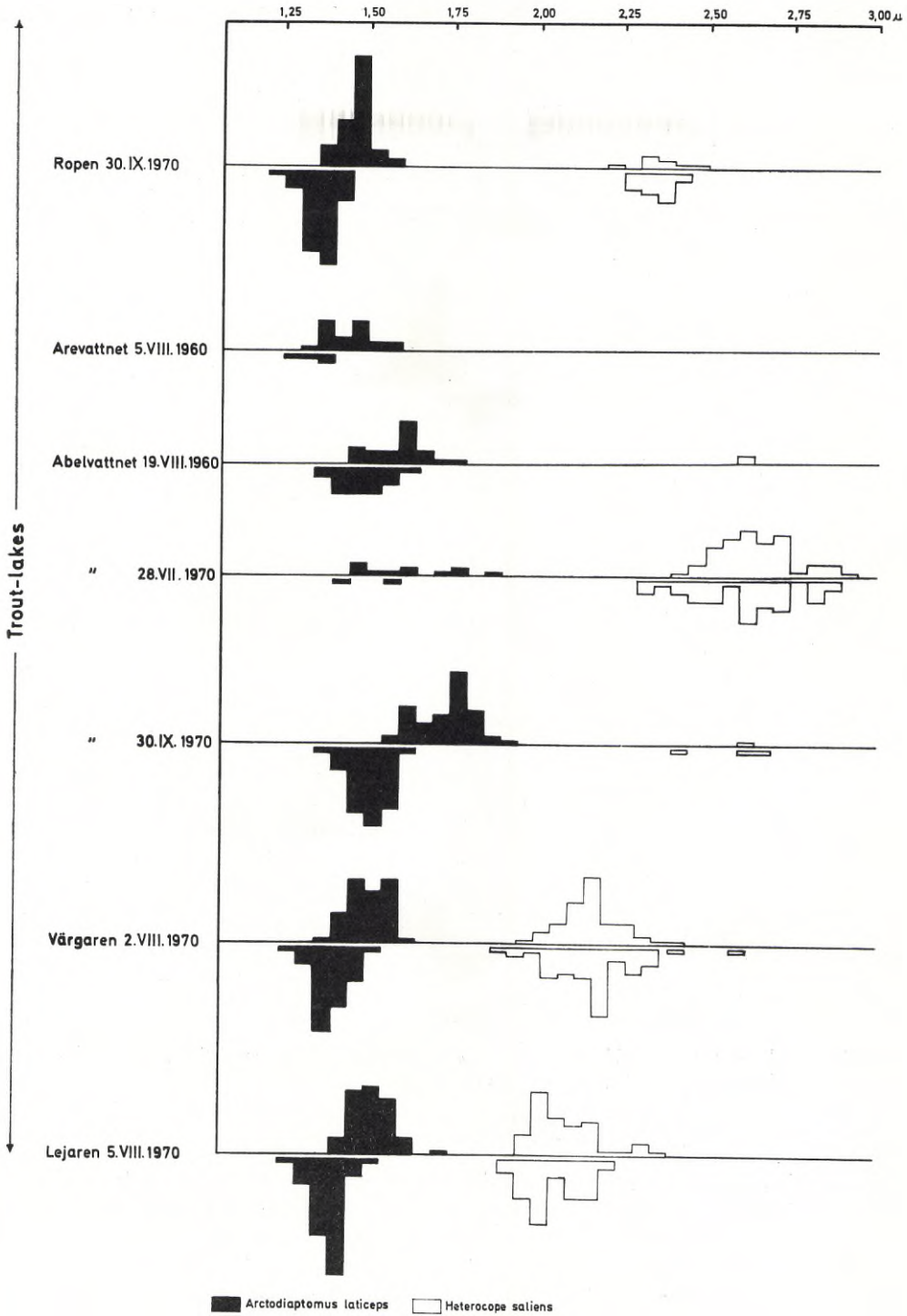


Fig. 7. Body length (cf. p. 53) of the calanoid copepods measured, females above and males below the central lines. Only mature specimens were

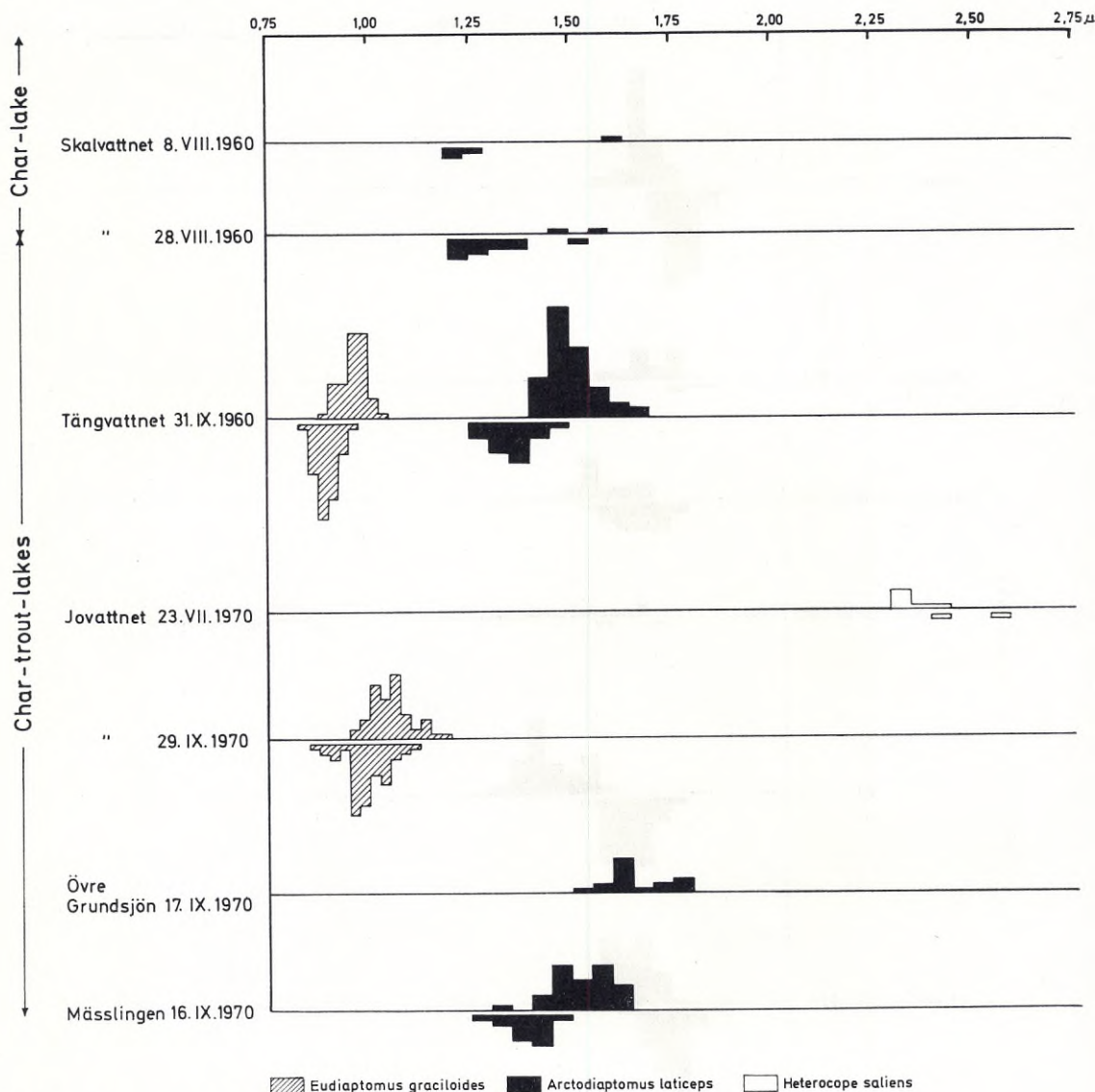


Fig. 8. Body length of the calanoid copepods in a char lake and certain trout lakes. Females above and males below the central lines.

extremely well-investigated Lake Stora Blåsjön (nor, of course, in the whitefish lakes still further downstream).

The conclusion may thus be drawn that *Daphnia longispina* s.str. "avoids" lakes containing planktivorous fish, while *Heterocope saliens* (as a population) endures (or escapes from) predation by char but not whitefish. *D. cristata*, *Ceriodaphnia qua-*

drangula, *Bosmina longirostris* and *H. appendiculata* can withstand predation from fishes of both these genera and are favoured in the lakes which they inhabit (possibly because competition from other zooplankters is eliminated). Other planktic crustaceans here discussed may also be influenced by fish predation, but not to the degree of near-extirmination, and therefore no conclusions

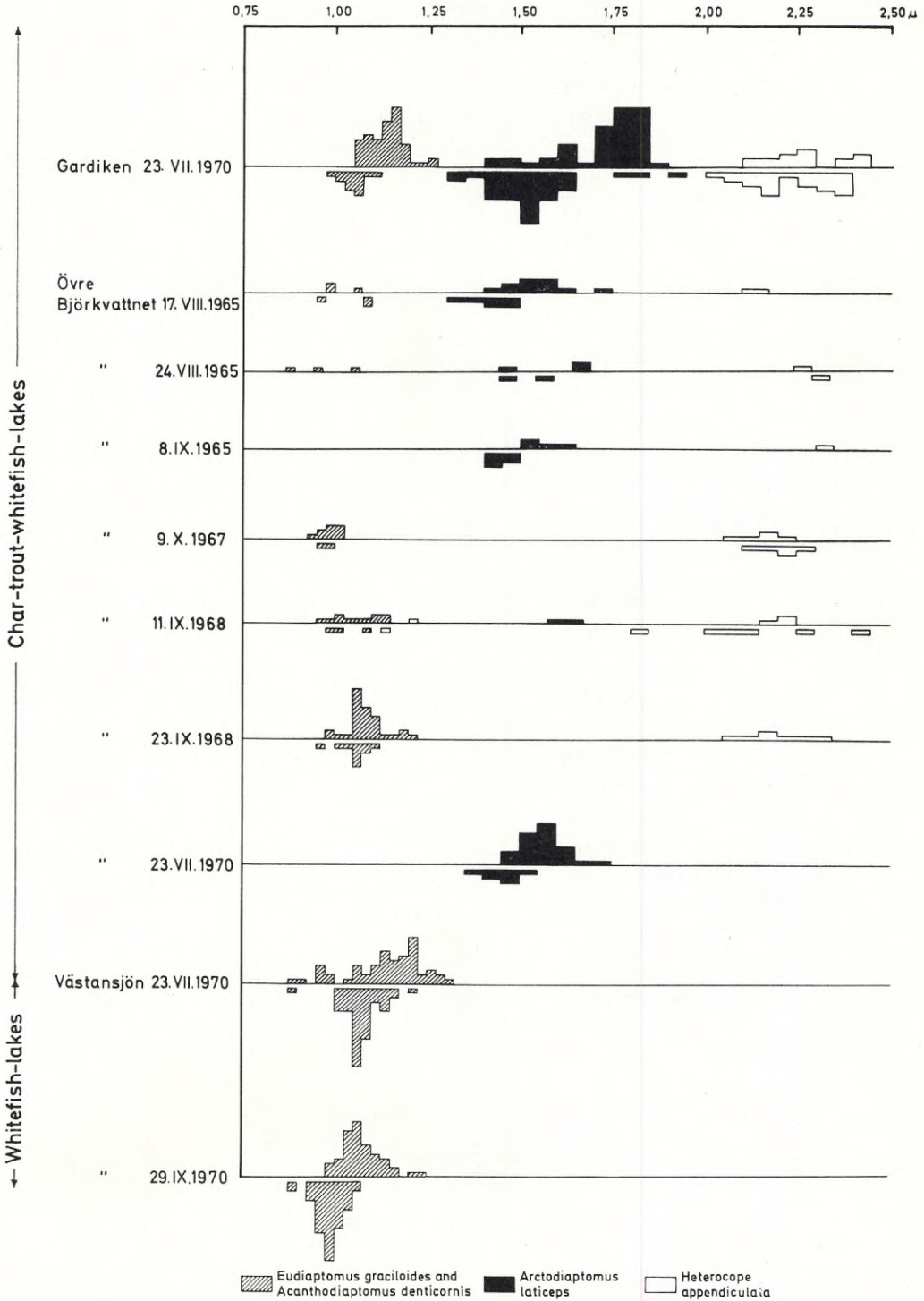


Fig. 9. Body length of the calanoid copepods in certain lakes containing whitefish. Females above and males below the central lines.

can be drawn with the aid of the rough and regional approach applied in this study.

Discussion

It appears from the exposition above that certain species are more sensitive than others to intense grazing by planktivorous fishes such as whitefish. Besides *Daphnia longispina* s.str. and *Heterocope saliens*, mentioned above, *Polyartemia forcipata* should also be discussed in this connection, though only two records are reported in Tables 2—3. Especially elucidative are the conditions of Lake Pieskejaure reported by NILSSON (1972a); as long as this lake was devoid of fish (except the sculpin *Cottus gobio* L.) *Polyartemia* occurred there in great numbers, but after the introduction of char the population was reduced to a minimum. In the period immediately following after the introduction it was demonstrated that *Polyartemia* constituted the main food of the char, the strong grazing effect thus being convincingly proved.

The question arises why precisely these three species should be especially sensitive to predation. There may be several factors involved, but two circumstances are so striking that attention should be drawn to them:

(1) The three species belong to the biggest members of the plankton, *Polyartemia* being the biggest phyllopod, *H. saliens* the biggest copepod. *Daphnia longispina* s.str. is surpassed by two other cladocerans (*Bythotrephes longimanus* and *Leptodora kindti*) as regards total length but probably not as regards dry weight. The effects of body size will be discussed in more detail in the next chapter.

(2) The three species in question are vividly coloured. This is especially conspicuous in the case of *H. saliens*, which is probably the most gaudily coloured species in the zooplankton of North Scandinavian lakes.¹ The description given

¹ *H. borealis* is probably comparable in this respect. It was not found by the present authors but was found in one of the lakes studied by LÖTMARKER (*op.cit.*). His find (included in Table 2) was made in Lake Överuman, a char-trout lake, and accords well with our argumentation.

by SARS (1903, p. 106) may be cited: "Body generally of a beautiful ultramarine hue, antennae, oral parts and urosome often tinged dark orange." The corresponding account of *H. appendiculata* may be compared with this (*loc.cit.* p. 109; the italics are ours): "Body semipellucid and generally of a light bluish green hue, anterior antennae and urosome in male tinged with orange."

Concerning *H. saliens*, we may also quote EKMAN (1904, p. 40): "Die Farbe der lebenden Tiere ist gewöhnlich im ganzen Cephalothorax, Abdomen und den Antennen des l. Paares rotbraun, an den Beinen blau, selten sind auch der Rücken und das Abdomen blau. Bei Exemplaren aus sehr kleinen Gewässern ist die Farbe bisweilen sehr dunkel: schwarzbraun und schwarzblau." The last sentence of this passage is of especial interest. The smallest water bodies of this region are mostly devoid of fish. There the zooplankters can consequently be vividly coloured without being exposed to the risk of being preyed upon by fish (and presumably not very much by other predators either).

The experiences of the cited authors agree completely with our own. We wish to draw special attention to some observations made in Lake Övre Heimdalsvann. In summer 1969 the Norwegian zoologist PETTER LARSSON and B. PEJLER were diving there in order to study the spatial distribution of larger zooplankters. The dominant crustaceans could fairly easily be distinguished from one another by sight alone, and even the colonies of *Conochilus* (Rotatoria) could be recognized. However, there was a quite remarkable difference in the ease with which the individual species could be discerned, *H. saliens* being by far the most conspicuous, partly on account of its great size but above all because of its vivid colouring.

The colour of *D. longispina* s.str. is not so vivid as that of *H. saliens* but is more pronounced than in the other cladocerans of the present material, according to the literature and to own observations. If we were to apply the original taxonomy proposed by SARS (1862, *cf.* PEJLER 1973) some or all of our populations should be assigned to his species *D. rosea*, characterized by its beautiful red colour. From SARS' Latin description the following may be cited (*op.cit.*, p. 21): "Testa colore roseo insignis parte imprimis superiore

saturato." The three "varieties" described by EKMAN 1904 which correspond to our "*D. longispina* s.str." are also characterized as more or less reddish. The two cladocerans *Bythotrephes* and *Lepidodora*, which are longer than *D. longispina*, are, on the other hand, completely colourless and transparent except for their big black eye, this often constituting the only means of detecting them macroscopically (according to, e.g., HERBST 1962 and our own experience).

The copepods are on average more visible than the cladocerans, the smaller cladocerans being quite transparent whereas the smaller calanoid copepods are more or less colourful, though never so much so as *H. saliens*. *Mixodiaptomus laciniatus*, which is rather rare in our material, is probably the most vividly coloured copepod if the *Heterocope* species are excepted (SARS 1903, EKMAN 1904 and own observations). According to the same sources, *Arctodiaptomus laticeps* and *Acanthodiaptomus denticornis* come next, while *Eudiaptomus graciloides* has, to cite SARS (*op.cit.*, p. 95) a "body generally very pellucid and almost colourless". *Cyclops scutifer* is either only faintly coloured or quite colourless.

On the whole the copepods are thus more highly coloured than the cladocerans. The disadvantage of a vivid colour plays, under these circumstances, a lesser rôle, possibly because they possess a more efficient escape behaviour.

The presence or absence of *H. saliens* ought to have secondary effects on the other zooplankters, as the members of this genus are "snatchers" ("Greifer" according to NAUMANN 1923) and largely predatory (see NAUMANN, *op.cit.*, ELSTER 1936, BURCKHARDT 1944, and BOSSONE and TONOLLI 1954). Of especial interest in this connection is the last-mentioned investigation, which shows that *H. saliens* has a severe grazing effect on *Arctodiaptomus bacillifer* (KOELB.), which in its turn reduces the competition on other filtrating calanoid copepods and thus allows *Acanthodiaptomus denticornis* to develop successfully. Coexistence of these two diaptomids is otherwise very rare, only one case being known from the many Alpine lakes which were studied in this connection.

In the present material, *A. denticornis* is often,

though not always, found together with some other diaptomid and with *H. saliens*. It seems difficult to draw any definite conclusions concerning the relations between *Heterocope* and diaptomids in our case. However, the same grazing effect ought to be exerted by planktivorous fish. Then it should be noted that two coexisting diaptomids were never found in the many lakes belonging to categories 1—3, but they occurred in about half of the lakes of categories 4—5, i.e. in the lakes where the predation from planktivorous fishes must be most intense.

As *Daphnia longispina* s.str. is a filter feeder (see HUTCHINSON 1967, p. 599 ff. and references), the secondary effects of its disappearance should be mainly in terms of reduced competition. It would appear, however, that not very much is known as to whether there are any differences in feeding habits between the separate *Daphnia* species, or between the separate genera of filter-feeding cladocerans on the whole (see HUTCHINSON, *op.cit.*, and EDMONDSON 1957).

The experiments carried out by HRBÁČKOVÁ-ESSLOVÁ (1963) indicate, however, that there may be some differentiation concerning food-particle size, the larger species utilizing on average larger particles. If this is so, *D. galeata*, which is the second largest *Daphnia* species, should be most favoured by the disappearance of *D. longispina* s.str. However, such a favouring can hardly be concluded from our material, inasmuch as *D. galeata* is found in some lakes together with *D. longispina* s.str. and is missing in the samples from several lakes without *D. longispina* s.str. It is true that the still smaller species *Daphnia cristata* and *Ceriodaphnia quadrangula* were found only (or almost only) in lakes of categories 5—6, from which *D. longispina* s.str. is missing; but this can hardly be explained by reduced competition from *D. longispina* s.str., especially when one considers the case of *D. galeata*.

As regards two of the species found only in whitefish lakes, viz. *Ceriodaphnia quadrangula* and *Bosmina longirostris*, attention will instead be drawn to another circumstance: besides being small, these species are normally characteristic of small lakes or ponds and of the littoral zone of larger lakes (see, e.g., WAGLER 1937, BERZINS 1958, Figs 9 and 11, PEJLER 1965, Fig. 38). The circumstances

should be compared with the interesting results obtained by BROOKS and DODSON (1965). These authors found *B. longirostris* and *Ceriodaphnia lacustris* to dominate in lakes with the planktivorous fish alewife, as a result of which the species of *Daphnia* and *Diaptomus*, otherwise dominating, were almost or completely excluded. BROOKS and DODSON (*op.cit.*, p. 28) explain this phenomenon in the following way: "The elimination of these pelagic zooplankters allows the primarily littoral species, such as *Bosmina longirostris*, to spread into the pelagic zone, from which we conclude, they would otherwise be excluded by their larger competitors." Though the larger filter-feeding crustaceans in our lakes are not so strongly suppressed as in the alewife lakes, an argumentation based on the same principle should be applicable to our material as well.

The zooplankters being preyed upon by planktivorous fishes and by *Heterocope* may be supposed to have developed adaptations for escaping their enemies. As concerns the cyclopids, their well-known positive rheotaxis should be important in this connection, as these copepods occur always in a much lower proportion in the stomach contents of planktivorous fishes than in the plankton samples from the water where the fishes concerned have collected their food (NILSSON 1955).

Regarding some rotifers it has been quite convincingly shown that long spines make them a much more difficult prey for *Asplanchna* and thus they are favoured by the selection in lakes containing the predator mentioned (see the footnote on p. 71 and the literature there referred to). The helmets of *Daphnia* may be conceived to have a similar function, and in this connection it is a striking fact that the only species lacking such a helmet altogether, *viz.* *D. longispina* s.str., appears to be the most sensitive to predation (*cf.* also JACOBS 1965). In Central and Southern Sweden this species is only found in ponds where predation from fishes should be relatively low as well (*cf.* PEJLER 1965 and STENSON 1972). This hypothesis as to the advantage of a helmet does not, of course, exclude the different explanation given by BROOKS (1968). Finally, *Holopedium gibberum*, another species apparently surviving fish predation, is possibly favoured by its voluminous gelatinous cover.

IV. THE EFFECTS OF THE BODY SIZE OF THE ZOOPLANKTERS

Results

It has already been mentioned that the species that are most sensitive to fish predation are among the biggest, while those only found in whitefish lakes are among the smallest (see also Figs 4—9 and Table 4). This becomes still more evident when members of the same genus are compared. The bigger *Heterocope* species, *H. saliens*, was collected almost exclusively in lakes of categories 1—4, the smaller species, *H. appendiculata*, only in whitefish lakes. The bigger *Bosmina coregoni* occurs in most samples, the smaller *B. longirostris* only in samples from whitefish lakes. The largest *Daphnia*, *viz.* *D. longispina* s.str., has been encountered only in lakes of categories 1—2 and 4, the smallest, *D. cristata*, only in categories 4—6 (and only in one lake of category 4), the medium-sized *D. galeata* in categories 2—6. *Ceriodaphnia quadrangula*, belonging to a related genus, is smaller than all *Daphnia* species and has been found only in lakes with whitefish. *D. pulex* (DEGEER), which is even bigger than *D. longispina*, was never found by us, but was encountered by EKMAN (1904) in smaller water bodies which were, so far as can be judged, devoid of fish.

The conditions within the diaptomid family are more obscure. Both *Arctodiaptomus laticeps* and *Eudiaptomus graciloides* occur in all categories of lakes, though the latter seems to play a greater rôle in whitefish lakes than does the former. In lakes of categories 1—3 the two species have never been found at the same time, as is often the case in other lakes. Where they do coexist, *A. laticeps* is bigger than *E. graciloides* (Figs 8—9), probably owing to selective feeding similar to that described by FRYER (1954) for *A. laticeps* and *E. gracilis*, a species very closely related to *E. graciloides*.

The infraspecific size variation of the species studied in this respect is rather wide, as emerges from comparisons both within and between the individual populations. It is very difficult to account fully for this wide variation, a great many complicated abiotic and biotic interactions probably being involved (*cf.* HUTCHINSON 1967 and references). However, when going from

“lower” to “higher” lake categories, as is done in Figs 4—9, it is quite apparent that the average size of the crustaceans involved becomes gradually smaller and that this change depends on infra-specific variation as well as on replacement of bigger species by smaller.

Discussion

The problem of body size of zooplankters in relation to nutritional relationships has been dealt with by HRBÁČEK and coworkers (e.g. 1958 and 1966; see also references in HUTCHINSON 1967, e.g. on p. 708—709), BROOKS and DODSON (1965), GALBRAITH (1967) and BROOKS (1968). The principles put forward in these papers are clearly applicable to our material as well. HRBÁČEK stated that rotifers were favoured in ponds with intense predation by planktivorous fish. It could not be decided whether this is true for our lakes as well, as the samples were collected with the aid of nets that were too coarse (see p. 53).

The distribution of individual crustacean species is in the papers mentioned (including the present one) mainly explained by the effect of biotic factors, in cases where previously abiotic factors, such as temperature, were brought into the foreground. Hutchinson (*op.cit.*, p. 694), after having discussed the altitudinal and latitudinal zonation in the *Calanoida*, arrives at the following conclusion: “The ecological interpretation of these distributions would appear impossible unless historic, biotic and competitive factors were considered, and the nature of such factors is almost completely unknown.” This was written before, e.g. GALBRAITH’s (1967) and BROOKS’ (1968) papers were published, and it might be said that the veil has now been lifted to some extent.

It should also be tested whether correlations with trophic degree could partly be explained in these terms. In this context the striking fact has been found that almost all the indicators of oligotrophy, according to PEJLER 1965, belong to the biggest species of their respective groups: all the biggest copepods, *viz.* *Heterocope appendiculata*, *Limnocalanus macrurus* SARS and *Eurytemora lacustris* (POPPE) were only found in connection with low-productive conditions. The two cladocerans considered as indicators of oligotrophy,

viz. *Limnosida frontosa* SARS and *Holopedium gibberum*, are among the biggest of their group. *Bythotrephes longimanus* and *Leptodora kindtii* are even longer, it is true, but in their case the body is extremely narrow and transparent. BROOKS (1968) considers the essential point to be the “visible size”, which in *Leptodora* is equivalent to the eye (*cf.* p. 66). Moreover, *B. longimanus* was only met with in oligotrophic lakes, but, as the finds were quite few in number, PEJLER did not venture to designate it as an indicator.

In the case of the genus *Daphnia*, conditions are not equally clear, but from a study of Figs 14—33 in PEJLER, *op.cit.*, it may be surmised that the individuals, irrespective of what species they belong to, are on average smaller in the more eutrophic lakes. Finally, the two rotifers indicating oligotrophy, *viz.* *Synchaeta grandis*, ZACHARIAS and *Ploesoma hudsoni* (IMHOF), are among the four biggest of the 52 species reported. *Asplanchna priodonta* GOSSE and *A. brightwelli* GOSSE (which are not considered indicators of any kind) have a still longer body, but they are very transparent, with the entrails loosely scattered (as in *Leptodora*), and therefore the dry weight may be suspected to be smaller than in *S. grandis* and *P. hudsoni*. In any case, the “visible size” (*cf.* BROOKS, *op.cit.*) is smaller in *Asplanchna* than in the two last-mentioned species. The eight species which are designated as true indicators of eutrophy are all rotifers, and thus small. As the grazing by planktivorous fishes should be greater in eutrophic than in oligotrophic lakes, these size correlations might be explained in the same manner as has been done above.

If this assumption is correct, a corresponding infraspecific variation might also be supposed to exist. From the data reported by WAGLER (1923), such a variation may be surmised concerning *D. cucullata*, bigger forms being found in large and more or less oligotrophic lakes. Regarding some rotifers, similar conditions apparently exist. Thus a correlation was established between body size of *Keratella cochlearis* (GOSSE) and lake transparency (transparency here being considered a crude indicator of primary production), the smallest forms being found in eutrophic lakes (PEJLER 1962). To judge from the literature (e.g. OLOFSSON 1917, ZENKEVITSCH and KONSTANTINOVA 1956) and our

Table 4. Length of body in the concerned crustaceans, according to literature.

	LILLJEBORG 1900	SARS 1903	RYLOV 1935	WAGLER 1937	KIEFER 1960	HERBST 1962	DUSSART 1967
<i>Holopedium gibberum</i> ♀ (excl. gelatinous cover)	1500—2200 µ		1500—2200 µ	up to 2500 µ			
<i>Daphnia longispina</i> s.str. ♀	1400—3000 µ		1500—3000 µ	c. 2500 µ		c. 2500 µ	
<i>Daphnia galeata</i> ♀	1400—2500 µ		up to 2500 µ				
<i>Daphnia cristata</i> ♀	880—1600 µ		880—1800 µ	c. 1600 µ		c. 1500 µ	
<i>Ceriodaphnia quadrangula</i> ♀	600—900 µ		600—900 µ	700—1400 µ		400—1400 µ	
<i>Bosmina coregoni</i> ♀	400—1000 µ		400—1000 µ	400—1200 µ		400—1500 µ	
<i>Bosmina longirostris</i> ♀	360—620 µ		400—600 µ	230—620 µ		up to 3000 µ	
<i>Bythotrephes longimanus</i> ♀	2000—5000 µ		2000—5000 µ	2000—3000 µ			
(excl. caudal spine)							
<i>Leptodora kindtii</i> ♀	up to 10000 µ		up to 12000 µ	c. 10000 µ		c. 10000 µ	
<i>Acanthodiaptomus denticornis</i>	♀ 2000 µ ♂ 1500 µ		♀ up to 3000 µ	♀ 2500—3000 µ ♂ 2000—2500 µ	1500—3000 µ		♀ 1000—3000 µ ♂ 1200—1500 µ
<i>Endiaptomus gracilis</i>	♀ 1400 µ ♂ 1200 µ		♀ 1000—1500 µ ♂ 1000—1200 µ	♀ up to 1500 µ ♂ 1000—1500 µ	up to 1500 µ		♀ 1000—1200 µ ♂ 1000—1200 µ
<i>Endiaptomus graciloides</i>	♀ 1300 µ ♂ 1000 µ		♀ 1100—1300 µ ♂ 1000—1100 µ	♀ up to 1300 µ ♂ 1000—1300 µ	up to 1300 µ		♀ 1200—1300 µ ♂ 1000—1200 µ
<i>Arctodiaptomus laticeps</i>	♀ 1800 µ ♂ 1400 µ		♀ 1220—1800 µ ♂ 1070—1400 µ				
<i>Mixodiaptomus laciniatus</i>	♀ 1600 µ ♂ 1400 µ		♀ 1050—2200 µ ♂ 1000—1600 µ		up to 2200 µ		♀ 1050—1200 µ ♂ 1400—1550 µ
<i>Heterocope appendiculata</i>	♀ 2200 µ		♀ 1800—2200 µ ♂ 2000—2200 µ	c. 2000 µ	c. 2000 µ		2000—2200 µ
<i>Heterocope borealis</i>	♀ c. 3000 µ		♀ 3000—5000 µ ♂ 2800—3300 µ	up to 5000 µ	c. 3000 µ		♀ 3000—5000 µ ♂ 2800—3300 µ
<i>Heterocope saliens</i>	♀ c. 3000 µ		♀ 2500—3200 µ ♂ 2200—2800 µ	up to 3000 µ	up to 3000 µ		c. 3000 µ
<i>Cyclops scutifer</i>			♀ 1200—1500 µ ♂ 1100—1200 µ	up to 3000 µ	up to 3000 µ		

own unpublished observations, a similar correlation may be suspected in *Kellicottia longispina* (KELLCOTT). In the case of the rotifers, such correlations can hardly be directly explained by fish predation, as these animals are probably too small to be caught in any high degree by planktivorous fishes. The larger size in oligotrophic lakes may be interpreted by applying BROOKS' and DODSON's size-efficiency hypothesis (see below), but as it is connected with longer spines it perhaps constitutes in addition an adaptation for escaping from predation by *Heterocope*.¹ *Heterocope* are mostly absent in samples from eutrophic lakes, a circumstance which may — if the argumentation above is followed — be due to predation by fish.

The "size-efficiency hypothesis" put forward by BROOKS and DODSON (*op.cit.*) implies, in agreement with WINBERG's law, that larger zooplankters have a better metabolic economy than do smaller ones, a property which must be an advantage in an environment poor in food, *i.e.* in oligotrophic lakes. Some results obtained by ZENKEVITSCH and KONSTATINOVA (*op.cit.*) are of interest in this connection: These authors found that the larger individuals of *Kellicottia longispina* from northernmost Russia exhibited a much slower locomotion than the smaller ones from the Moscow region. *K. longispina*, faintly indicating oligotrophy according to PEJLER 1965, p. 474, moves on the whole much more slowly than the smaller euryecious *Keratella cochlearis*, of which the smallest form, *f. tecta*, indicates eutrophy and exhibits especially lively movements (observations by B. PEJLER in Central Swedish lakes, *e.g.* Lake Erken and Lake Lilla Ullevifjärden). EDMONDSON (1965) found a lower reproductive rate in *Kellicottia longispina* than in *Keratella cochlearis*, a fact which ought to be quite consistent with those

mentioned above. In conclusion it may be said that it appears that the predation by planktivorous fishes also has secondary effects on such zooplankters as are not eaten, including the rotifers (*cf.* HRBÁČEK *et al.* 1961).

V. PLANKTON AS FOOD OF BROWN TROUT, CHAR AND WHITEFISH

Most species of freshwater fish in Scandinavia feed on plankton at some stage of life. Categorizing roughly the species dealt with here, we may be allowed to make the following generalizations:

Brown trout:

Can be planktivorous as fry and fingerling when living in or near the outflow of lakes where planktic crustaceans are washed out (NILSSON 1957). Allopatric populations of brown trout (*i.e.* not living together with any other fish species) also sometimes feed to a great extent on planktic crustaceans (NILSSON 1965, KLEMETSEN 1967, AASS 1969). In a collection of 19 samples of allopatric trout recorded by NILSSON (1965), however, only 2 were dominated by *Cladocera*. In a series consisting of 52 samples from 13 lakes with brown trout sympatric with arctic char, none was dominated by zooplankton; on the contrary, as many as 32 samples contained no zooplankters at all. This was explained by, among other things, a more efficient zooplankton consumption by char, leading to a food segregation between the two species (NILSSON 1960).

In fact brown trout, like other species of the genus *Salmo*, have the mouth and gillraker region better adapted to relatively large prey: they have teeth on the vomer also and the gillrakers are few, short and tap-shaped. Thus one would presume that zooplankton would only be eaten by trout when being very abundant or otherwise easily available. In our material there is nothing to indicate that the introduction of brown trout into a barren lake would change the composition of zooplankton (*cf.* Fig. 10).

The zooplankters consumed are mainly large-sized ones, as shown by several Scandinavian authors. For instance, the predominant species recorded by

¹ That a *Heterocope* population can have a strongly decimating effect on smaller crustaceans as well as on rotifers was reported by BURCKHARDT (1944). For *Kellicottia* its long spines appear to be an advantage in this respect, since they are seldom found in the stomachs of the predatory rotifer *Asplanchna*, while other rotifers of similar size are often preyed upon (see NAUWERCK 1963 and EDMONDSON 1965). DE BEAUCHAMP (1952a, 1952b), POURRIOT (1964) and GILBERT and WAAGE (1967) have found an increase of the spine length in some other rotifer species when *Asplanchna* was present.

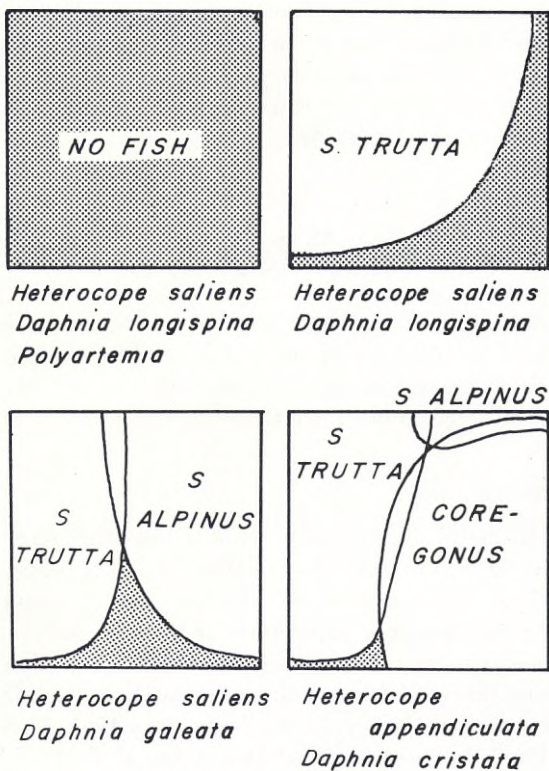


Fig. 10. Simplified model of the "dimensions" of the niches of brown trout, arctic char and whitefish in allopatry and sympatry, and the larger dominant species of zooplankton.

NILSSON (1960, 1961, 1965) from many Swedish lakes have been *Bythotrephes longimanus* and *Eurycerus lamellatus* MÜLL., and AASS (1969) found that, in 48 samples of brown trout from Norwegian lakes feeding on *Crustacea*, 19 were dominated by *Eurycerus*, 10 by *Bythotrephes* and 3 by *Daphnia* (the rest by the large bottom-dwelling *Lepidurus arcticus* PALLAS). KLEMETSEN (1967) studied a population of brown trout (Lake Jølster-vann, Norway) with very pronounced habits of plankton feeding. In that case *Daphnia galeata*, *Bosmina obtusirostris* and *Bythotrephes longimanus* were recorded as being the most important food items.

Arctic char:

Are planktivorous throughout life up to a size of 40 cm or even more (NILSSON 1964). Allopatric

char, however, tend to prefer bottom food like brown trout. In 17 samples of allopatric char examined by NILSSON (1965) only one was dominated by zooplankton. In the above-mentioned series of 52 samples from 13 lakes with sympatric char, 36 were dominated by zooplankton. It is thus obvious that char, in the presence of bottom-feeding species, are apt to segregate into a "planktivore niche".

The morphology of the mouth and gillraker region of char is also of a less "predatory" type than is that of brown trout. Vomeral teeth are found only in the front end of the mouth and the gillrakers are longer and more numerous than in brown trout. NILSSON and FILIPSSON (1971) found the gillraker count of char to vary between 19 and 27 in a North Swedish lake, and McPHAIL stated 25 to be the mean for North American arctic char.

Arctic char on the whole consume smaller species of *Crustacea* than do brown trout (cf. NILSSON 1955, 1960, 1961). Large species, like *Eurycerus lamellatus*, *Holopedium gibberum* and *Bythotrephes longimanus*, are certainly important, but in most cases recorded, *Daphnia galeata* and *Bosmina coregoni* are the most frequent species. *Heterocope* is frequent as food during certain seasons, but *Diatomus* and *Cyclops* occur only occasionally as food of adult char.

Whitefish:

Occur as five species in Scandinavia, but the specific relationships within the genus *Coregonus* are very complicated because of frequent hybridization. Introgression "enters the evolutionary process and destroys the effects of speciation in the past but also creates new dissimilarities by a sort of subspeciation" (SVÄRDSON 1970). The only stable specific character seems to be the number of gillrakers which in Swedish populations varies between 19 and 50. As a rule, the whitefish lakes are inhabited by either two or more species or else by hybrids with very variable gillraker counts.

It has long been accepted that the number and length of the gillrakers can be correlated with the feeding of the whitefish. Individuals with long and numerous gillrakers (and so, also, little space between gillrakers) tend to feed on small particles, for instance, planktic crustaceans. This rule, how-

ever, is not without exceptions (SVÄRDSON 1950, NILSSON 1958, KLIEWER 1970), and a considerable plasticity within species due to interaction with other species has been noted (NILSSON 1960, LINDSTRÖM and NILSSON 1962). As a complex, however, the whitefish populations must have an extraordinary impact on the zooplankton composition, as there are in every whitefish lake age groups or subpopulations that are very efficient planktivores.

Many Scandinavian investigations have shown that among the zooplankters consumed by most species of *Coregonus*, *Bosmina coregoni* is by far the most important food item. For instance, LINDSTRÖM (1962) showed that *Bosmina* was the predominant food for the young of three co-existing species of whitefish in Northern Sweden. Adult whitefish, too, are known to utilize *Bosmina* as the main food item. For example, NILSSON (1958, 1960) recorded *Bosmina* as being one of the predominant food items of three species of whitefish even after the fish had reached a size of 15 cm.

Species with very sparse sets of gillrakers (e.g. *C. pidschian*) have also appeared to utilize *Bosmina* as their main food up to a size of 150 mm (NILSSON 1958). Other planktic crustaceans noted by, for instance, LINDSTRÖM (1962) have been *Daphnia*, *Holopedium* and *Polyphemus*, albeit in relatively small frequencies as compared with *Bosmina*.

VI. FEEDING OF RECENTLY INTRODUCED CHAR AND WHITEFISH

Very few investigations as to the initial food habits of recently introduced char and whitefish have been recorded. We have already mentioned the interesting events that happened when arctic char were introduced into an almost barren lake in Northern Sweden (Lake Pieskejaure, p. 66). Here what was apparent was that the intruders chose the most available and sizable food items.

The following table (partly from KARLSSON and NILSSON 1968) gives the tendency as to the consumption of planktic *Crustacea* over the years investigated.

Crustacean food of char from Lake Pieskejaure. Mean percentage of stomach volume (from KARLSSON and NILSSON 1968).

Year	1967	1968	1969
<i>Polyartemia</i>	40.2	—	—
<i>Bythotrephes</i>	0.8	0.9	—
<i>Polyphemus</i>	—	0.3	—
<i>Bosmina</i>	—	—	7.9
<i>Daphnia</i>	—	—	0.4

It appears that during the three years investigated the food habits of the recently introduced char changed from large, easily caught species to smaller ones (like *Bosmina* and *Daphnia*).

NILSSON and FILIPSSON (1971) recorded the food of recently introduced whitefish into a lake previously only inhabited by brown trout and by two species of arctic char (cf. above p. 72). The table below, extracted from their paper, indicates a predominance of *Holopedium gibberum* and the large semibenthic species *Eurycerus lamellatus* during the first years of invasion, and an increasing share of the smaller species *Daphnia galeata* and *Bosmina coregoni* in more recent years.

Food of whitefish from Lake Övre Björkvattnet (from NILSSON and FILIPSSON 1971). Mean percentage of stomach volume.

Year	1964	1965	1967	1968
<i>Eurycerus lamellatus</i>	31.1	46.6	30.9	20.9
<i>Daphnia galeata</i>	10.7	9.6	15.5	25.4
<i>Bosmina coregoni</i>	—	8.0	10.0	25.2
<i>Bythotrephes longimanus</i>	0.9	2.6	2.6	—
<i>Holopedium gibberum</i>	47.0	5.1	7.3	14.7

In principle this table is closely comparable with that demonstrating the food of the recently introduced arctic char. Large and easily available species are heavily exploited during the first years after the new fish species have been introduced. After that the latter have to turn to smaller and less available species, like *Daphnia* and *Bosmina*.

The conclusion we have to draw from these two examples is that fish, like other animals, exploit what is most rewarding at the moment, but overgrazing forces them to segregate into their "niches", to specialize on what they can best survive on in difficult competitive situations.

VII. CONCLUSIONS

In the previous sections we have discussed in some detail the possible significance of fish predation on the zooplankton composition in North Swedish lakes. A rough but logical correlation between colour, behaviour and size of the zooplankters and the presence of zooplankton-feeding fish has convinced us that fish predation is in many cases the factor ultimate in governing the presence or absence of certain species of crustaceans. This is in good agreement with what has been observed by BROOKS and DODSON (1965), GALBRAITH (1967) and other authors, about the effects of introductions of plankton-feeding fish.

Fig. 10 gives a very simplified model of the above-mentioned correlation. Large-sized, colourful species of crustaceans such as *Daphnia longispina* s.str. and *Heterocope saliens* dominate in barren lakes or in lakes with brown trout alone.

The first of the two species mentioned was never found in any lake containing char or whitefish, where it is apparently replaced by the smaller, more transparent species *D. galeata*. In the same way *H. saliens* is replaced by *H. appendiculata* (smaller and less conspicuously coloured) in the whitefish lakes. In lakes containing whitefish, the smallest species, such as *Daphnia cristata*, *Ceriodaphnia quadrangula* and *Bosmina longirostris*, become more or less predominant. The intra-specific variation is more obscure, but when considered together with the species composition there is no doubt that it contributes towards the decreasing average size of the zooplankters along the series of lake categories sketched above (e.g. in Figs 4—9).

In spite of frequent human transplantations of fish, there still exists in Northern Sweden a relatively simple zonation of species from the arctic highlands to the boreal coniferous forest areas and the Baltic coastal region, the sequence roughly being: barren lakes — allopatric trout or char lakes — sympatric trout and char lakes — whitefish lakes (mostly with several other species) — lakes with pike, perch and "coarse fish".

The competitive replacement of arctic char by whitefish recorded in so many cases should occur as an interaction in fairly early stages when the species involved are all planktivorous. Certain

whitefish species seem to be more disastrous to char than are others, and many cases of coexistence between whitefish and certain char species (or subspecies) have been recorded. It still remains to study in detail the mechanisms involved in this replacement process. It seems, however, fairly obvious that there is a tendency for most recently introduced species to turn to the largest and most easily available prey, a tendency which can lead to a very rapid overexploitation or perhaps even extinction. The fact that there exist "typical" food items for certain species thus does not necessarily mean that the typical prey also represents the most highly-prized food for the species in question.

It may be appropriate to state that we do not believe that there is inevitably a complete extinction of planktic crustacean species as new planktivorous fish species are introduced, but rather that predation combined with interaction with other zooplankters has made them so rare that they escape both predation by fish and sampling. The very rapid exchange, for instance, in the representation of *Heterocope* in Lake Övre Björkvattnet from the large-sized *H. saliens* to the small-sized *H. appendiculata* after the invasion of whitefish supports the idea that the latter species may have been present — albeit in small populations or in refugia — even before the invasion.

The structure of the specific fish populations should also play an important part. For instance, stunted char populations or whitefish with dense gillrakers should have a different impact on the zooplankton community than that of sparse populations of large-sized char or whitefish populations consisting of bottom-feeding species with few gillrakers. We can thus expect many exceptions from the general model here presented.

VIII. ACKNOWLEDGEMENTS

We gratefully acknowledge Professor GUNNAR SVÄRDSON who initiated this investigation and gave us all sorts of vigorous support.

The drawings were made by Mrs NANNA GUSTAFSSON, the measurements by Mrs NANNA GUSTAFSSON, Mr I. JÖHANSSON and Mr B. MOLIN.

Part of the plankton sampling was carried out by Messrs S. ANDREASSON, O. FILIPSSON, E. FISK, B. GRÖNLUND, R. KARLSSON, G. KJELLBERG and T. SJÖSTRÖM. Mrs. B. ERICSSON brought a final order to our manuscript.

IX. REFERENCES

- AASS, P. 1969. Crustacea, especially *Lepidurus arcticus* PALLAS, as brown trout food in Norwegian mountain reservoirs. *Rep. Inst. Freshw. Res. Drottningholm* 49: 183—201.
- AXELSON, J. 1961. Zooplankton and impoundment of two lakes in Northern Sweden (Ransaren and Kultsjön). *Rep. Inst. Freshw. Res. Drottningholm* 48: 84—168.
- BEAUCHAMP, P. M. DE 1952a. Un facteur de la variabilité chez les Rotifères du genre *Brachionus*. *C. R. Acad. Sci., Paris* 234: 573—575.
- 1952b. Variations chez les Rotifères du genre *Brachionus*. *C. R. Acad. Sci., Paris* 235: 1355—1356.
- BERZINS, B. 1958. Ein planktologisches Querprofil. *Rep. Inst. Freshw. Res. Drottningholm* 39: 5—22.
- BOSSONE, A. and V. TONOLLI 1954. Il problema della convivenza di *Arctodiaptomus bacillifer* (KOELB.), di *Acanthodiaptomus denticornis* (WIERZ.) et di *Heterocope saliens* LILLJ. *Mem. Ist. ital. Idrobiol. de Marchi* 8: 81—94.
- BRELIN, I. and I. JÓHANSSON, in press. Studier rörande Stora Blåsjöns pelagiala kräftdjursplankter, med särskild hänsyn till utveckling i samband med Mysis-introduktion och vattenreglering. *Inform. Inst. Freshw. Res. Drottningholm*. (Mimeographed in Swedish with English summary.)
- BROOKS, J. L. 1957. The systematics of North American *Daphnia*. *Mem. Conn. Acad. Arts Sci.* 13. 180 p.
- 1968. The effects of prey size selection by lake planktivores. *Syst. Zool.* 17: 273—291.
- and S. I. DODSON 1965. Predation, body size and composition of plankton. *Science* 150: 28—35.
- BURCKHARDT, G. 1941. Esistono forme intermedie fra "le due specie di *Bosmina*"? (Gibt es Verbindungsglieder zwischen "den beiden *Bosmina*-Species"?) *Schweiz. Z. Hydrol.* 9: 128—148. (In Italian, with German summary.)
- 1944. Verarmung des Planktons in kleinen Seen durch *Heterocope*. *Schweiz. Z. Hydrol.* 10(1): 121—124.
- DAHL, K. 1920. Studier over røje i ørretvand. *Norsk Jaeger- og Fiskeforb. Tidskr.* 49. 16 p.
- DUSSART, B. 1967. Les copépodes des eaux continentales. Paris I. 500 p.
- EDMONDSON, W. T. 1957. Trophic relations of the zooplankton. *Trans. Amer. micr. Soc.* 76(3): 225—245.
- 1965. Reproductive rate of planktonic rotifers as related to food and temperature in nature. *Ecol. Monogr.* 35: 61—111.
- EKMAN, S. 1904. Die Phyllopoden, Cladoceren und freilebenden Copepoden der nordschwedischen Hochgebirge. *Zool. Jb. System.* 21(1): 1—170.
- 1910. Om människans andel i fiskfaunans spridning till det inre Norrlands vatten. *Ymer* 30: 133—140.
- 1957. Die Gewässer des Abisko-Gebietes und ihre Bedingungen. *K. svenska Vetensk. Akad. Handl. ser. 4, 6(6)*. 172 p.
- ELSTER, H. J. 1936. Einige biologische Beobachtungen an *Heterocope borealis* FISCHER (= *H. weismanni* IMHOF). *Int. Rev. Hydrobiol.* 33: 357—433.
- FRYER, G. 1954. Contributions to our knowledge of the biology and systematics of the freshwater Copepoda. *Schweiz. Z. Hydrol.* 16: 64—77.
- GALBRAITH, M. G., Jr. 1967. Size-selective predation on *Daphnia* by rainbow trout and yellow perch. *Trans. Amer. Fish. Soc.* 96(1): 1—10.
- GILBERT, J. J. and J. K. WAAGE 1967. Asplanchna, Asplanchna-substance and posterolateral spine length variation of the rotifer *Brachionus calyciflorus* in a natural environment. *Ecology* 48(6): 1027—1031.
- HERBST, H. V. 1962. Blattfusskrebse (Phyllopoden: Echte Blattfüsser und Wasserflöhe). Stuttgart. 130 p.
- HJELM, C. 1972. Sammanställning av professor Sven Ekmans undersökningar av kräftdjursplankton i Torneträskområdet. *Inform. Inst. Freshw. Res. Drottningholm* (6). 17 p. (Mimeographed in Swedish.)
- HOLMGREN, S. 1968. Phytoplankton production in a lake north of the Arctic Circle. *Scripta Limnol. upsal.*, Coll. 5 (1969). Scriptum 236. 42 p. 24 Tables and 82 Figs.
- HRBÁČEK, J. 1958. Typologie und Productivität der teichartigen Gewässer. *Verh. int. Ver. Limnol.* 13: 394—399.
- M. DVOŘÁKOVÁ, V. KOŘINEK and L. PROCHÁZKOVÁ 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. *Verh. int. Ver. Limnol.* 14: 192—195.
- and M. HRBÁČOVÁ-ESSLOVA 1966. The taxonomy of the genus *Daphnia* and the problem of "biological indication". *Verh. int. Ver. Limnol.* 16: 1661—1667.
- HRBÁČKOVÁ-ESSLOVA, M. 1963. The development of three species of *Daphnia* in the surface water of the Słapy Reservoir. *Int. Rev. Hydrobiol.* 48(2): 325—333.
- HUITFELDT-KAAS, H. 1906. Planktonundersøgelser i norske vande. Christiania. 199 p. (In Norwegian, with German summary.)
- HUTCHINSON, G. E. 1967. A treatise on limnology. Vol. 2: Introduction to lake biology and the limnoplankton. New York, London and Sydney. 1, 115 p.
- JACOBS, J. 1965. Significance of morphology and physiology of *Daphnia* for its survival in predator-prey experiments. *Naturwissenschaften* 52: 141—142.

- KARLSSON, R. and N.-A. NILSSON 1968. Rödingen och örtingen i Pieskejaure. Nedbetning av näringsfaunan i en tidigare fisktom sjö. *Inform. Inst. Freshw. Res. Drottningholm* (14). 19 p. (Mimeographed in Swedish.)
- KIEFFER, F. 1960. Ruderfusskrebse (Copepoden). Stuttgart. 97 p.
- KLEMETSEN, A. 1967/68. On the feeding habits of the population of brown trout (*Salmo trutta* L.) in Jølstervann, West Norway, with special reference to the utilization of planktonic crustaceans. *Nytt Mag. Zool.* 15: 50—67.
- KLIEWER, E. V. 1970. Gillraker variation and diet in lake whitefish *Coregonus clupeaformis* in Northern Manitoba. In: *Biology of Coregonid Fishes* Eds.: C. C. LINDSEY, C. S. WOODS. Univ. Manitoba Press Winnipeg p. 147—165.
- LANGELAND, A. 1972. A comparison of the zooplankton communities in seven mountain lakes near Lillehammer (1896 and 1971). *Norweg. J. Zool.* 20: 213—225.
- LIEDER, U. 1957. Beiträge zur Kenntnis des Genus *Bosmina* (Crustacea, Cladocera) IV. Versuch einer Monographie der Untergattung *Enbosmina* Seligo 1900. Diss. Berlin. 247 p.
- LILLJEBORG, W. 1900. *Cladocera Sueciae*. Uppsala. 701 p. and 87 plates.
- LINDSTRÖM, T. 1951. Sur l'écologie du zooplankton Crustacé. *Rep. Inst. Freshw. Res. Drottningholm* 33: 70—165.
- 1958. Observations sur les cycles annuels des planctons crustacés. *Rep. Inst. Freshw. Res. Drottningholm* 39: 99—145.
- 1962. Life history of whitefish young (*Coregonus*) in two lake reservoirs. *Rep. Inst. Freshw. Res. Drottningholm* 44: 113—144.
- and N.-A. NILSSON 1962. On the competition between whitefish species. In: *The Exploitation of Natural Animal Populations* Eds.: E. D. LE CREN and M. W. HOLDGATE. Oxford. p. 326—340.
- LÖFFLER, H. 1953. Beitrag zur Planktonkunde des Faxälv-Systems. *Rep. Inst. Freshw. Res. Drottningholm* 34: 58—72.
- LÖTMARKER, T. 1964. Studies on planktonic crustacea in thirteen lakes in northern Sweden. *Rep. Inst. Freshw. Res. Drottningholm* 45: 113—189.
- MC PHAIL, J. D. 1961. A systematic study of the *Salvelinus alpinus* complex in North America. *J. Fish. Res. Bd. Canada* 18(5): 193—814.
- NAUMANN, E. 1923. Spezielle Untersuchungen über die Ernährungsbiologie des tierischen Limnoplanktons. II. *Acta Univ. Lund*, nov. ser., avd. 2, 19(6). 17 p.
- NAUWERCK, A. 1963. Die Beziehungen zwischen Zooplankton und Phytoplankton im See Erken. *Symb. bot. upsal.* 17(5). 163 p.
- 1967. Das Latnjajaureprojekt. *Rep. Inst. Freshw. Res. Drottningholm* 47: 56—75.
- NILSSON, N.-A. 1955. Studies on the feeding habits of trout and char in North Swedish lakes. *Rep. Inst. Freshw. Res. Drottningholm* 36: 163—225.
- 1957. On the feeding habits of trout in a stream of Northern Sweden. *Rep. Inst. Freshw. Res. Drottningholm* 38: 154—166.
- 1958. On the food competition between two species of *Coregonus* in a North-Swedish lake. *Rep. Inst. Freshw. Res. Drottningholm* 39: 146—161.
- 1960. Seasonal fluctuations in the food segregation of trout, char and whitefish in 14 North-Swedish lakes. *Rep. Inst. Freshw. Res. Drottningholm* 41: 185—205.
- 1961. The effect of water-level fluctuations on the feeding habits of trout and char in the Lakes Blåsjön and Jormsjön, North Sweden. *Rep. Inst. Freshw. Res. Drottningholm* 42: 238—261.
- 1964. Effects of impoundment on the feeding habits of brown trout and char in Lake Ransaren (Swedish Lappland). *Verh. int. Ver. Limnol.* 14: 444—452.
- 1965. Food segregation between salmonoid species in North Sweden. *Rep. Inst. Freshw. Res. Drottningholm* 46: 58—73.
- 1967. Interactive segregation between fish species. p. 295—313. In: *The Biological Basis of Freshwater Fish Production*. Ed.: S. D. GERKING. Blackwell, Oxford.
- 1972. Effects of introductions of salmonids into barren lakes. *J. Fish. Res. Bd. Canada* 29(6): 693—697.
- and O. FILIPSSON 1971. Characteristics of two discrete populations of Arctic char (*Salvelinus alpinus* (L.)) in a north Swedish lake. *Rep. Inst. Freshw. Res. Drottningholm* 51: 90—108.
- OLOFSSON, O. 1917. Süßwasser-Entomotraken und -Rotatorien von der Murmanküste und aus dem nördlichsten Norwegen. *Zool. Bidr. Uppsala* 5: 259—294.
- PEJLER, B. 1962. On the variation of the rotifer *Keratella cochlearis* (GOSSE). *Zool. Bidr. Uppsala* 35: 1—17.
- 1965. Regional-ecological studies of Swedish freshwater zooplankton. *Zool. Bidr. Uppsala* 36: 407—515.
- 1973. On the Taxonomy of Limnoplanktic *Daphnia* Species in Northern Sweden. *Zoon* 1(1): 23—27.
- POURRIOT, R. 1964. Étude expérimentale de variations morphologiques chez certaines espèces de rotifères. *Bull. Soc. zool. Fr.* 89: 555—561.
- RYLOV, W. M. 1935. Das Zooplankton der Binnengewässer. *Binnengewässer* 15. 272 p.
- SARS, G. O. 1862. Om de i Omegnen af Christiania forekommende Cladocerer. II. *Forh. Vidensk. Selsk. Christiania* 1861. 54 p. (In Latin and Norwegian.)
- 1903. An account of the Crustacea of Norway. IV: *Copepoda Calanoida*. Bergen.
- SMITH, S. H. 1964. Status of the deepwater cisco population of Lake Michigan. *Trans. Amer. Fish. Soc.* 93: 155—163.

- STENSON, J. A. E. 1972. Fish predation effects on the species composition of the zooplankton community in eight small forest lakes. *Rep. Inst. Freshw. Res. Drottningholm* 52: 132—148.
- SVÄRDSON, G. 1950. The Coregonid problem II. Morphology of two Coregonid species in different environments. *Rep. Inst. Freshw. Res. Drottningholm* 31: 151—162.
- 1954. Sibling species in the genus *Coregonus*. *St. Naturvetenskapl. Forskningsråds Årsb.* 7: 135—140.
- 1961. Rödningen. *Fiskefrämjandets Årsbok Fiske* p. 25—37.
- 1970. Significance of introgression in Coregonid evolution. In: *Biology of Coregonid Fishes* (Eds.: C. C. LINDSEY, C. S. WOODS). Univ. Manitoba Press, Winnipeg p. 33—59.
- WAGLER, E. 1923. Über die Systematik, die Verbreitung und die Abhängigkeit der *Daphnia cucullata* von physikalischen und chemischen Einflüssen des Milieus. *Int. Rev. Hydrobiol.* 11: 41—88, 262—316.
- 1937. Crustacea Krebstiere. *Die Tierwelt Mitteleuropas*, Bd. 2, Lief 2a. 224 p.
- WELLS, LARUE 1970. Effects of alewife predation on zooplankton population in Lake Michigan. *Limnol. Oceanogr.* 15(4): 556—565.
- ZENKEVICH, L. A. and M. I. KONSTANTINOVA 1956. Locomotion and the motor system of Rotifera. *Zool. Zh.* 35: 345—364. (In Russian.)

Estimates of Age, Growth, Standing Crop and Production of Salmonids in Some North Norwegian Rivers and Streams

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I. INTRODUCTION

Information about growth and production of salmonids in different environments is of considerable interest today. Sports and commercial fisheries are increasing their demands on these species while other activities, such as hydroelectric developments, are changing the environment. North Norway is one of the places where it is possible to study fish populations in an almost undisturbed environment. Descriptions of natural populations are needed to provide data for comparison with populations that develop in modified environments. Knowledge of fish production and the conditions which influence it in different environments is valuable to those trying to manage fisheries resources. This work was undertaken in an attempt to provide some of this basic information. Five river systems were examined. In Finnmark there were: Komagelva in north Varanger; Storelva in Laksefjord and Russelva in Revsbotn. In Troms there was Breivikelva in Ullsfjord, and in Nordland, Leirskarelva a tributary of the Rossaga which flows into Sorfjord. In addition to these rivers a number of small streams were sampled and these are included in the results which follow.

II. METHODS

None of the methods of estimating the size of stream populations of fish seemed suitable for use in this study. A method was needed that required a minimum of personnel and equipment and could be executed in a few hours.

In 1963 the intention was to select and delimit

each sampling area with fine meshed stop nets, seine, mark and release all fish captured and then rotenone to get a complete kill. Sample areas were chosen in places where rotenone would be quickly neutralized by dilution. The technique proved impractical because seining was not effective over the stony bottoms and in the clear water of the sampling areas. However it quickly became apparent that, used carefully, rotenone could provide information that otherwise would be difficult and costly to obtain. The major drawbacks to its use are that sample sites have to be carefully chosen and the rates of recovery of fish are difficult to estimate. Advantages are speed and portability, all sizes of fish are affected and at least minimal estimates of the standing crop of fish in the sample areas are obtained.

In 1966 it was hoped to overcome some of the drawbacks to the use of rotenone. The plan was to enclose sample areas with barrier nets of 4 mm square mesh, use electrofishing gear to mark a portion of the population and use rotenone to recover as many fish as possible from the areas. Rotenone was inactivated downstream with potassium permanganate. Preliminary tests in some small streams east of Komagelva showed the available electrofishing gear was ineffective probably because of low water conductivity. Instead the following procedure was adopted. A barrier net was placed across the downstream end of the sample area. Rotenone was slowly added at the upstream end and sufficient $K Mn O_4$ was distributed below the net to turn the water quite purple for at least 25 minutes. As soon as fish began moving to the surface they were caught in a dip net, the dorsal fin was clipped and they were released. As many fish as possible were marked

Table 1. Locations of rotenone samples where at least 6 marked fish were recaptured in the sample.

Location, and sample	Date (1966)	Number Marked	Number Recaptured	Percentage Recovered	Size of Sample less Sticklebacks	Percentage of sample Marked
Trib. of Komagelva KT 6	14 July	23	14	61	115	12
Komagelva K 5	18 July	17	9	53	40	22
Komagelva K 4	18 July	74	50	68	312	16
Trib. of Komagelva KT 2	19 July	18	11	61	137	8
Trib. of Komagelva KT 3	19 July	45	36	80	215	17
Trib. of Komagelva KT 4	20 July	54	45	83	117	38
Komagelva K 2	20 July	70	46	66	158	29
Trib. of Storelva SL 1	24 July	70	41	59	520	8
Trib. of Storelva SB 1	25 July	9	8	89	20	40
Trib. of Storelva SL 2	26 July	22	15	68	93	16
Storelva S 1	27 July	18	10	55	94	11
Ravddulelva Rav 2	29 July	50	37	74	200	19
Ravddulelva Rav 4	30 July	38	20	53	36	56
Ravddulelva Rav 3	1 Aug	21	17	81	83	20
Russelva Rus 4	2 Aug	33	27	82	68	40
Russelva Rus 3	3 Aug	8	6	75	44	14
Russelva Rus 2	3 Aug	26	21	81	139	15
Russelva Rus 1	3 Aug	46	39	85	92	42
Strupskarelva St 3	9 Aug	8	6	75	20	30
Strupskarelva St 2	11 Aug	33	22	67	66	33
Strupskarelva St 1	11 Aug	13	8	61	17	47
Leirskarelva L 3	23 Aug	18	12	67	261	5
Leirskarelva L 1	24 Aug	131	90	70	437	21
Leirskarelva L 4	24 Aug	59	50	85	329	15
Trib. of Leirskarelva LT 1	24 Aug	45	31	69	118	26
Totals		949	671	70.7		

and released while they were still swimming. When most fish were too disoriented to continue marking, collecting began. An attempt was made to recover every fish in the sample area.

This technique worked well in some locations but in others it failed because not enough fish could be marked. It was best in long sample areas where the current was not too swift and impractical in short swift sample areas. The method is subject to certain obvious criticisms. Only fish disoriented by rotenone can be captured and marked. These fish will die and be available for recovery but any fish which were unaffected by the rotenone will not be found. If there is a complete kill this criticism is not as important although some fish upon first contact with the rotenone may hide themselves in inaccessible places and never be seen. Recovery is less if marking is attempted than if collection starts immediately rotenone is added. This is because the initial response of affected fish is to swim at the surface

where they are easily visible and in the later stages of asphyxiation they sink and often get swept under rocks and into crevices where they may be overlooked. More small fish are lost this way than large fish so that the proportion of small fish is underestimated.

The advantage of marking is that it provides an estimate of the rate of recovery so that minimum standing crop figures (*i.e.* the numbers actually collected) can be corrected and an estimate of the actual standing crop obtained. In practice no fry and very few 1+ year class fish were marked. The recovery rates obtained in this study apply to fish above 65 mm fork length. The recovery rates estimated will generally be high for fish younger than 2+ years old.

In order to calculate realistic confidence intervals for a population estimate it is necessary to mark and recover a large proportion of the population. Using the technique described this was not often possible. At the same time experience

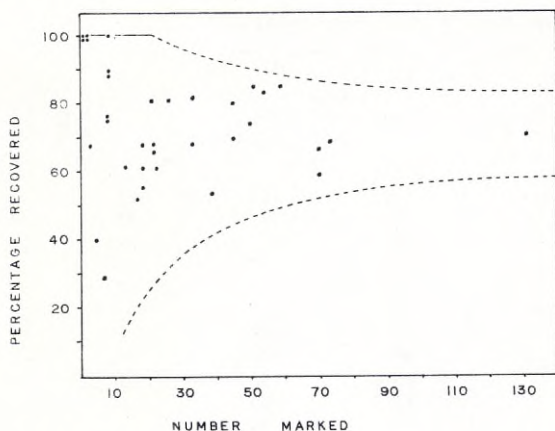


Fig. 1. The percentage of marked fish recovered compared with the number marked.

suggests the results are biologically meaningful and reasonably accurate. Twenty-five samples were taken in 1966 in which at least 6 marked fish were recaptured. The recapture rate in these samples varied between 53 % and 89 %. Details are given in Table 1. The percentage of marked fish recaptured was not so variable as the locations and conditions of sampling would suggest. The recovery rate in Leirskarelva, a glacial river with very turbid water and bad visibility, was almost the same as in Komagelva where conditions for recovery appeared ideal. It is not easy to judge the recovery rate from the appearance of a sampling area. An exception was the sample taken in Ravddulelva July 30, 1966. Here physical structure of the habitat — flattened, irregular stones with numerous crevices — offered abundant hiding places and many fish were never found. The percentage of marked fish recovered was the lowest of any sample.

Fig. 1 presents the data from all samples in which marking was attempted. Where more than 10 fish were marked the recovery rate was between 50 % and 85 %. Where very few fish were marked the recovery rate was more variable and limits are suggested by the dotted lines in the figure which were drawn freehand. The mean recovery rate of marked fish in all samples included in Table 1 was just above 70 %. Taking these results into account the data were treated in the following way. Where information on

recovery rate was available, *i.e.* the samples included in Table 1, the minimum standing crop was the number and proportion of fish actually recovered. The estimated standing crop was the number recovered adjusted for the estimated recovery rate with the numbers of fry and 1+ fish increased to equal the adjusted number of 2+ fish. Where no information was available from marking, the estimated standing crop was calculated from the minimum standing crop as described, using a 70 % recovery rate. It was felt these adjustments were realistic and the estimated values would be within ± 15 % of the true values. In the results the greatest errors are in the estimated numbers of fry and 1+ fish, here the corrections are too conservative. This means figures for numbers of fish per unit area are too low but values for weight of fish per unit area and production are more accurate since very small fish contribute little to the biomass or production.

In all samples fish collected were placed immediately in 5 % formalin and stored for at least 2 weeks until hardened. The preservative was then drained off and the moist fish packed in plastic bags and shipped to Canada for study. Upon arrival the 1963 material was thoroughly washed and stored in 40 % isopropyl alcohol until examined 2—4 months later. The 1966 material was stored in plastic bags until washed for study 3—7 months later. Each of the larger specimens was weighed to the nearest 0.1 g and the fork length measured to the nearest 1.0 mm. Sex and state of maturity was noted. A total egg count was obtained for a few almost mature resident char and egg size estimated by measuring three rows of ten eggs. Fry were measured individually, weighed in groups. Fry and 1+ fish were not sexed.

Ages of the youngest fish were obtained by recognition of fry and 1+ or yearling fish, occasionally 2+ fish. Ages were confirmed for all except fry by scale reading for salmon and most trout and by examination of the otoliths of char, (NORDENG 1961). In these northern populations from small rivers and glacial streams scale reading gives results which are consistently one year too young unless it is recognized that the first annulus is generally absent or at the most first year growth is represented by only 2—3 circuli.

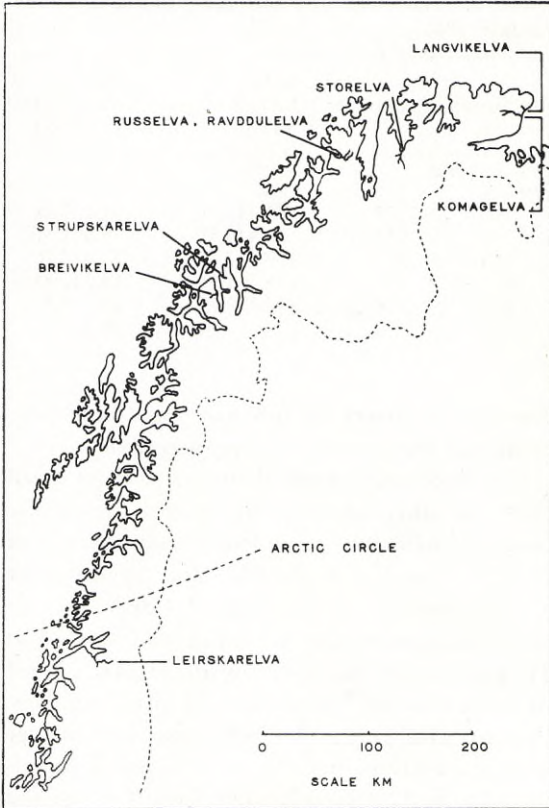


Fig. 2. The location of sampling sites in north Norway.

Fortunately length frequency distributions, in the present study, provide an easy method of checking the accuracy of the scale reading so that the results are not in doubt. Trout from Leirskarelva had both scales and otoliths examined as scales proved difficult and perhaps unreliable for age determination while otoliths were much clearer. It has been generally accepted that otoliths of fish preserved in formalin are unsuitable for age determination. This was not true for this material. The only problem encountered was that some of the fish taken early in the summer of 1966 were improperly preserved and in these the otoliths disintegrated. In all other samples the otoliths were dissected out, cleaned, allowed to clear (usually in glycerine) and viewed by dissecting microscope. Growth bands were well defined and ages agreed with length frequency groupings in the samples. Most of the fish dealt with were

young and this may account for the ease with which the otoliths could be interpreted.

Growth curves obtained from rotenone samples may be slightly flattened by an upward bias in the estimated size of the youngest age groups and by absence of some of the largest and more aggressive members of the older age groups from the sample areas. These errors should not be great and are probably less than those resulting from other sampling methods, especially for the youngest age groups. Mortality rates based on the proportions of fish in the different age groups are invalid for fry and yearlings and may be for 2+ year old fish because of inadequate recovery of small fish. These weaknesses in the data should be considered when interpreting the results.

Production was calculated on an annual basis using the estimated standing crop figures for the numbers of fish in each age group and the mean weights for each age group derived from analysis of the total sample. The graphical method described by ALLEN (1951) was used to calculate production and since the major part of the production comes from fish of age 2+ and older the total estimated production is thought to be fairly accurate. Results are expressed as grams produced per 100 square meters per year which facilitates comparisons between samples and locations.

III. RESULTS

The results are presented by watershed, starting in east Finnmark and working west and south. Locations of the main watersheds are shown on the map, Fig. 2. Only five species of fish were encountered, these were: salmon, *Salmo salar*; trout, *Salmo trutta*; char, *Salvelinus alpinus*; three-spined stickleback, *Gasterosteus aculeatus*; and nine-spined stickleback, *Pungitius pungitius*. These will be referred to by common name in the text with the note that salmon refers to the parr stage and that stickleback means three-spined. *P. pungitius* was encountered in only one location and is referred to as *P. pungitius*.

Langvikelva

This small river, about 9 km long, enters Varanger just east of Langbunes (Fig. 3). The source is

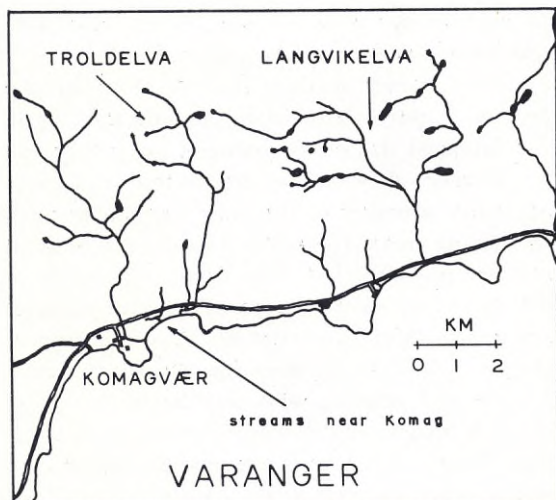


Fig. 3. Langvikelva, Troldeleva and the streams near Komagvaer.

about 190 m above sea level and the river flows in a steep sided cut in an open shallow tree-less valley. A single large sample was obtained from an area 330 m long, the downstream end of which was 500 m distance from the sea. At this point Langvikelva averages 30 m wide and 10 cm deep. The bed is rock-strewn and boulders protrude above 20 to 30 % of the surface. On July 12, 1966 when the sample was taken, the water temperature was 14°C, the current was swift and the water level appeared somewhat above the summer norm. The sample was obtained primarily to test the effectiveness of $K\ Mn\ O_4$ in neutralizing

Table 3. Age and size of char in Langvikelva, 12 July 1966.

Age Group	Number	Mean Length mm S.D. in ()	Mean Weight gm S.D. in ()
Fry 0+	1	26	0.2
1+	77	52.4 (5.2)	1.3 (0.4)
2+	211	86.4 (6.5)	5.6 (1.3)
3+	203	109.8 (7.0)	12.1 (2.7)
4+	154	125.2 (5.9)	18.3 (2.9)
5+	30	144.8 (7.7)	28.7 (5.1)
6+	2	170	44.0

rotenone. Recovery of fish may have been poor because of the current and type of bottom.

The river contains an abundant stock of small char, no other species were taken. The sample contained 678 char, a minimum standing crop of 7 or 76.0 gm of fish per 100 sq.m. Adjusting for a 70 % recovery of fish of age 2+ and older the estimated standing crop was calculated to be 15 or 113 g of fish per 100 sq.m. For the reasons alluded to above this may be low. Details of the numbers, biomass, and production both total and by age groups are given in Table 2. Production is estimated to be 72 g per 100 sq.m. Details of age and size are given in Table 3. Growth is very slow in this stream and early in their sixth summer the char average only 15 cm fork length and 29 g weight. No mature female char were taken in the collection, it was too early in the summer, but a number of fish were showing clear signs of gonadal development. Amongst the females this was more

Table 2. The numbers, biomass and production of char in Langvikelva, 12 July 1966, area 9,900 sq.m.

Age group	Standing Crop				Production grams
	Minimum		Estimated		
	Number	Biomass g.	Number	Biomass g.	
0+	1	.2	302	60	60
1+	77	106.2	302	393	333
2+	211	1192	302	1705	1312
3+	203	2453	290	3508	1932
4+	154	2826	220	4041	1623
5+	30	860	43	1230	1250
6+	2	88	3	126	595
Totals	678	7524	1462	11184	7105
Totals per 100 sq. m	7	76	15	113	72

Table 4. The age and size of char in Troldeiva, Troldeiva, 11 July 1966.

Age Group	Number	Mean Length mm S.D. in ()	Mean Weight gm S.D. in ()
0+	32	23.3 (2.0)	0.16
1+	56	55.3 (4.3)	1.7 (0.3)
2+	10	86.8 (6.5)	6.8 (1.8)
3+	11	104.8 (5.0)	12.1 (2.4)
4+	3	130 —	21.5 —
5+	2	164 —	45.3 —
6+	1	186 —	36.5 —

obvious than amongst the males. The proportions of maturing females in the different age groups were: 1+ fish, 0 out of 34; 2+ fish, 0 out of 86; 3+ fish, 20 out of 117; 4+ fish, 31 out of 71; 5+ fish, 12 out of 12; 6+ fish, 1 out of 1. The proportions of males showing signs of maturing were: 1+ fish, 0 out of 43; 2+ fish, 0 out of 125; 3+ fish, 2 out of 86; 4+ fish, 21 out of 83; 5+ fish, 12 out of 18 and 6+ fish, 1 out of 1. One can deduce from this data that a small proportion of the char in Langvikelva spawn towards the end of their fourth summer (age 3+) but it is probably not until the end of the sixth summer (age 5+) that all fish reach maturity. Sex ratios derived from this data show an equal proportion of males and females amongst fish aged 3+ and older. A predominance of males amongst the 2+ fish is probably a result of errors in sexing these small immature fish.

This stream flows into the sea just east of Komagvaer (Fig. 3). Its source is about 220 m above sea level and it is about 7 km long. Its drainage area is about half that of Langvikelva hence the stream is smaller. It flows in a deep channel cut into an open tree-less valley. A sample was obtained from a section of the stream 156 m long, average width 3.5 m and average depth 25 cm, located 750 m from the sea. The bed of the stream consists of rounded stones some of which are quite large. The stream contains a dense population of small char, no other species were taken. In addition to the sample, some fish were taken below the barrier net as the rotenone was improperly neutralized. These fish have been used to provide additional data on sex ratios and fecundity.

Table 4 gives the age and size of char taken in the sample area. Growth is slow and corresponds to that observed in Langvikelva. Table 5 summarizes the information on numbers, biomass and production of char in Troldeiva. The numbers and biomass correspond to a minimum density of 21 fish weighing 83 g per 100 sq.m. Assuming a 70 % recovery of fish from the sample area the estimated standing crop is 36 fish weighing 111 g per 100 sq.m. Production is estimated at 94 gm per 100 sq.m. per year.

Sex ratios of char taken in Troldeiva were not significantly different than a 1 : 1 ratio. The male to female ratios observed were: 1+ fish, 92 : 72; 2+ fish, 16 : 21; 3+ fish, 14 : 12; 4+ fish, 5 : 5; 5+ fish, 0 : 4; 6+ fish, 1 : 0. On 11 July females

Table 5. The numbers, biomass and production of char in Troldeiva, 11 July 1966, area 546 sq.m.

Age group	Standing Crop				Production grams
	Minimum		Estimated		
	Number	Biomass	Number	Biomass	
0+	32	5.1	80	12.8	12.8
1+	56	95.0	80	136.0	136.0
2+	10	67.7	14	95.2	207.0
3+	11	133.1	16	193.6	77.5
4+	3	64.4	4	86.0	60.0
5+	2	48.7	2	48.7	20.0
6+	1	36.5	1	36.5	
Total	115	450	197	609	513
Total per 100 sq.m.	21	83	36	111	94

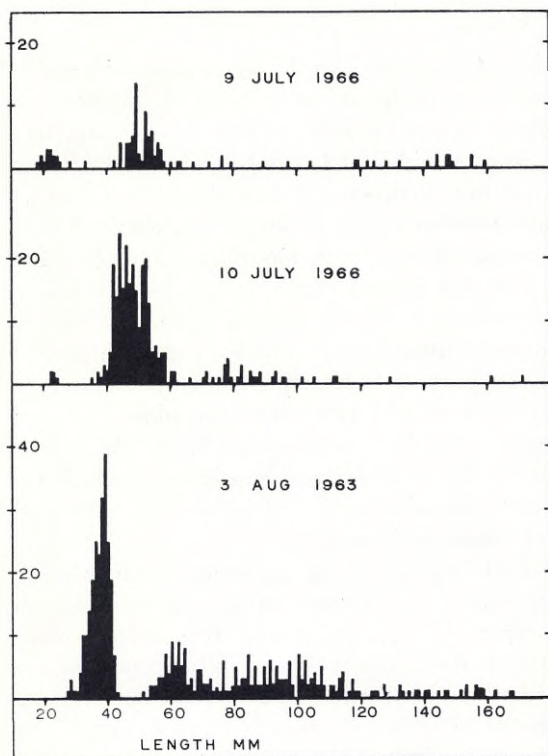


Fig. 4. The length frequency distributions of char samples taken in the streams near Komagvaer.

showed more evidence of impending spawning than males. One female aged 3+, 4 aged 4+ and 3 aged 5+ had developing ovaries, while 2 males aged 4+ and 1 aged 6+ were ripening. Three females had ovaries in an advanced state of maturation and egg counts indicate the fecundity as follows:

Age 3+	113 mm	13.8 g	102 eggs
Age 5+	142 mm	34.0 g	146 eggs
Age 6+	142 mm	31.5 g	174 eggs

These results correspond with those observed in neighbouring streams and are apparently typical of the char populations inhabiting streams and small rivers in east Finnmark.

Streams near Komag

East of Komagvaer two very small streams drain the coastal flats, both are less than 700 m in length. They join on the shore and flow in a shallow

Table 6. Age and size of char in streams near Komagvaer. (A) 3 August 1963; (B) 9 July 1966; (C) 10 July 1966.

Age and Sample	Number	Mean Length mm S.D. in ()	Mean Weight gm S.D. in ()
A 0+	234	38.1 (2.0)	0.62
B 0+	5	23.8 (0.7)	0.16
C 0+	17	23.6 (3.5)	0.12
A 1+	84	63.5 (5.4)	2.82 (0.8)
B 1+	248	48.9 (4.9)	1.3 (0.3)
C 1+	66	52.1 (4.3)	1.5 (0.2)
B 2+	26	80.9 (6.7)	5.2 (1.3)
C 2+	7	80.4 (9.5)	5.0 (2.5)
B 3+	7	102.8 (7.1)	11.1 (2.5)
C 3+	1	105	12.6
B 4+	1	130	19.0
C 4+	4	124	32.3
B 5+	1	162	38.1
C 5+	9	145 (5.0)	33.7 (5.0)
B 6+	1	172	33.0
C 6+	3	157	45.7

depression across the sand. Above the high water mark they have cut channels through the sand and shore grasses. For a few hundred meters the channels are clearly visible, then they divide into small branches and disappear in the shore vegetation. The streams support an apparently vigorous char population which was sampled in 1963 and 1966. A sample obtained 3 August, 1963 from the larger stream contained: 478 char (2,805 g); 10 sticklebacks and 6 *P. pungitius*. A sample, extending further upstream was obtained from the same area on 9 July, 1966. It contained 289 char (634 g). A third sample taken in the smaller stream 10 July 1966 contained 74 char (682 g). Analysis of the data is difficult because between 1963 and 1966 the char population in the larger stream had not recovered from the 1963 sampling which may have removed more than half the population. In addition, not all the fish in the 1963 collection were aged and the interval, about 3 weeks, between collections in the two years resulted in a size differential between fry in the two collections which suggested that about half the annual growth increment was achieved during this three week period. These changes are shown in the length frequency histograms for the three collections in Fig. 4. Table 6 summarizes the information on ages and sizes of char in the collections.

Table 7. Reproductive potential of char in streams near Komagvaer, 3 August 1963; 10 July 1966.

	Length mm	Weight gm	Age	Egg Diameter mm	Number of Eggs
<i>Aug. 3, 1963</i>					
	157	44.8	—	3.4	223
	147	34.6	—	3.7	130
	154	36.1	—	3.2	120
	141	32.6	—	3.5	170
	168	52.4	—	3.4	217
	158	47.4	—	3.6	153
	139	29.9	—	3.5	164
	128	25.9	—	3.2	75
	152	42.4	—	3.8	221
	134	32.4	—	3.7	112
	142	28.3	—	3.3	198
	169	60.3	—	3.9	266
<i>Means</i>	<i>149</i>	<i>39</i>		<i>3.5</i>	<i>171</i>
<i>July 10, 1966</i>					
	149	36.2	5+	—	186
	148	38.0	5+	—	135
	145	37.7	5+	—	167
	150	39.6	5+	—	197
<i>Means</i>	<i>148</i>	<i>38</i>	<i>5+</i>	<i>—</i>	<i>171</i>

Two of the collections contained maturing female char the reproductive potential of which is given in Table 7. The mean egg count is very low, but the females in the 3 August collection contained over 2,000 eggs, more than enough to produce the fry taken in the collection. With such low individual fecundity, if the population is to maintain itself, each egg must have a higher probability of surviving to maturity than in more fecund populations. This reduces loss of energy in reproductive products and from an ecological point of view may be an efficient way for a

population to conserve energy in a marginal habitat.

Estimation of production in these samples was done by assuming a 70 % recovery rate and, by assigning ages to the larger fish in the 3 August sample, using the char that were aged to produce an age-length key. The results are given in Table 8. Comparison of the 3.8.63 and 10.7.66 samples gives an indication of the difference resulting from taking the sample later in the season when the fish are growing rapidly, the 10.7.66 area was probably not affected by the 63 sampling, being in

Table 8. The minimum standing crop, estimated standing crop and production of char in streams near Komagvaer.

Sample	Area sq.m.	Minnum Standing crop/100 sq.m.		Estimated Standing crop/100 sq.m.		Estimated Production g/100 sq.m. Year
		Number	Biomass g	Number	Biomass g	
3.8.63	750	64	373	91	531	368
9.7.66	850	34	75	90	107	97
10.7.66	218	34	313	101	389	201

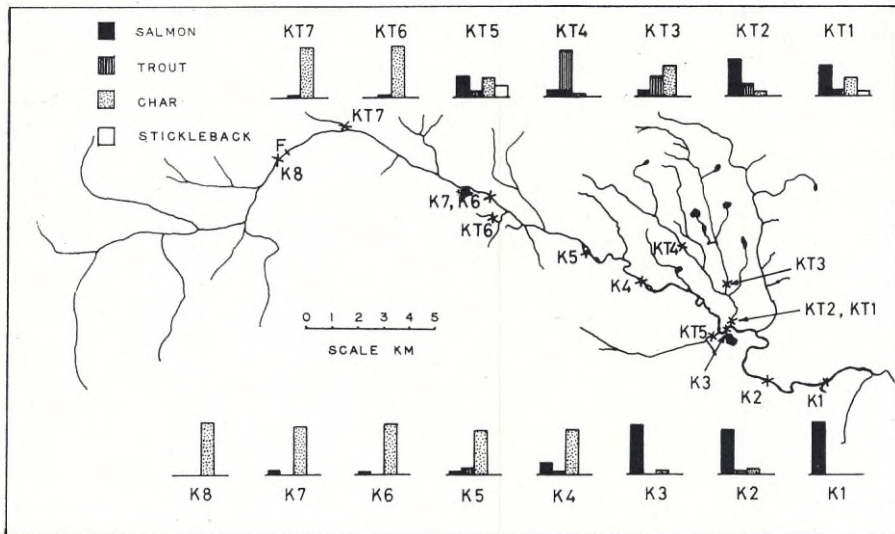


Fig. 5. Sampling sites and the proportions of fish species in collections from Komagelva and tributaries.

an almost separate stream. Estimated production increases from 201 g/100 sq.m./year in the earlier sample to 368 g/100 sq.m./year in the later one. The changed age structure of the population in the area sampled in 1963 and resampled in 1966 resulted in estimated production being approximately halved. The sample taken 9.7.66 gave an estimated production of 97 g/100 sq.m./year, compared with 201 for the unaffected population a day later. How long it will take the char populations in these small streams to recover is unknown but at the least it will probably be 6–10 years.

Komagelva

This river rises at an altitude of over 400 m and flows in an easterly direction to discharge into Varanger Fiord at Komagvaer. BERG (1946) provides details of the river and its salmon production. The drainage area is about 337 sq.km., the river 31 km long. The valley is open and treeless, the river alternating between pools and shallow rapids. The river bed is predominantly gravel and small stones interspersed with larger stones and appears fairly stable. There are no severe rapids, the first obstacle to fish migration is the falls marked on Fig. 5. In the lower part of the valley the river has cut through a flat plain and flows in a wide shallow channel between steep banks.

There are many good spawning and feeding areas for salmon and in recent years the river has been a consistently good producer. Anglers have taken nearly 6000 kg of salmon a year, the majority weighing between 1.5 and 5 kg. There is also a good stock of sea-char and sea trout. The tributary streams generally have gravel or stony bottoms except where they cut through peat deposits in the flat valley floor near the main river. Here they have vertical peat banks, stone, gravel, sand or peat beds, and in places are overhung by small willow shrubs. The water is very clear and in spite of the northerly latitude temperatures of up to 16°C were recorded in July in the main river, tributary streams were a few degrees cooler as was the main river in the upper reaches.

The river was sampled in 1963 and again in 1966 when more extensive work was possible. Eight samples, K1–K8 were obtained in the main river and seven, KT1–KT7 in tributary streams. The distribution of sampling sites is shown in Fig. 5. Sample K1 was obtained by angling, Sample K3 was an accidental kill of fish in the main river which resulted from an overdose of rotenone in a tributary stream (Sample KT5). All other samples were meant to be quantitative although only 9 proved suitable for calculations of productivity.

Table 9. Samples, species composition and minimum standing crop, Komagelva and tributary streams.

Sample	Date	Area sq.m.	Number of Fish by Species				Minimum Standing crop/100 sq.m.	
			Salmon	Trout	Char	Stickleback	Number	Biomass g.
K1	31.7.63	Angling	38	—	—	—	—	—
K2	20.7.66	2,000	135	7	16	—	8	83
K3	30.7.63	Accident	89	—	5	—	—	—
K4	18.7.66	2,100	66	14	232	—	15	67
K5	18.7.66	512	2	5	33	—	8	181
K6	1.8.63	3,500	16	—	568	—	17	67
K7	14.7.66	3,500	31	1	402	—	12	49
K8	15.7.66	?	—	—	18	—	—	—
KT1	29.7.63	2,400	145	26	80	23	11	54
KT2	19.7.66	1,520	92	32	13	—	9	51
KT3	19.7.66	1,332	19	83	113	—	16	214
KT4	20.7.66	1,260	19	96	2	—	9	165
KT5	30.7.63	1,300	43	11	34	27	9	96
KT6	14.7.66	530	—	1	114	—	22	205
KT7	15.7.66	900	—	4	179	—	20	—
Totals			695	280	1,809	50		

Some collections were too small, e.g. K5, 40 fish; K8, 18 fish; KT5, 115 fish mixed species; and one collection, KT7, was unsuitable because of faulty preservation.

A list of sampling stations, giving the area sampled, date, number of fish obtained and minimum standing crop is given in Table 9. Figure 5 shows the composition of the fish fauna at the various sampling stations. Young salmon predominate in the first 8 km of the main river and in the lower parts of the larger tributaries but quickly disappear above this. In the main river they are replaced by char. In the lower tributaries either trout or char may be dominant but in tributaries higher up the valley it is char. Very few trout were taken in the main river. Temperature and size of stream may be important in influencing distribution although the data are insufficient to show this. The warmest tributaries, when sampled, were the ones with the most trout, e.g. KT4, 14.6°C; KT3, 14.4°C, as compared to KT6, 11.5°C and KT7, 11.0°C. There are no physical barriers to prevent salmon extending their range much farther up the main river than they do. They occupy the lower valley where slightly higher temperatures may give them a competitive advantage over char.

Details of age and size of fish in the samples are given in Table 10, salmon; Table 11, trout;

and Table 12, char. The tables include data selected from the larger age group samples only. Inspection of the tables shows that it is difficult to give a composite picture of growth of the three species because there are differences in different parts of the system and even greater differences between years, the 1963 collections having been taken about two weeks later than those in 1966. Samples taken during the same year show a trend towards slower growth in the upper parts of the system. For example in 1966 4+ salmon had a mean length of 111 mm in Sample K2, 104 mm in Sample K4 and 96 mm in Sample K7. Char age 1+ had a mean length of 61 mm in Sample K4, 59 mm in Sample K7 and 50 mm in Sample K8. Between years differences are great because growth is rapid in July. At the same place, KT1 and KT2, 1+ salmon were 37 mm in 1966 and 46 mm in 1963 when the sample was taken 10 calendar days later. This indicates a growth increment of about 1 mm/day. The figures for 2+ salmon are: 62 mm in 1963 and 75 mm in 1966, a growth increment of 1.3 mm/day. For trout taken in the same location the figures are: in 1966 1+ trout were 47 mm, in 1963 53 mm, daily increment 0.6 mm; in 1966 2+ trout were 78 mm, in 1963 they were 91 mm, daily increment 1.3 mm. For char the best comparison is given by Samples K6 and K7. K6 was taken in 1963, 18 calendar days

Table 10. *The age and size of salmon parr in Komagelva and tributaries.*

Sample	Date	Age	Number	Length mm	S.D.	Weight g.	S.D.
K1	31.7.63	4+	30	127	7.5	—	—
		5+	5	139	2.7	—	—
K2	20.7.66	1+	9	40	2.2	0.7	—
		2+	12	70	4.3	3.9	0.8
		3+	66	86	6.4	7.2	1.6
		4+	37	111	11.1	15.1	4.8
		5+	11	130	8.8	24.4	5.3
K3	30.7.63	1+	10	48	1.8	1.4	—
		2+	56	76	4.0	4.8	0.7
		3+	22	108	6.9	13.8	3.0
K4	18.7.66	3+	36	85	8.0	6.4	1.8
		4+	18	104	5.0	11.2	1.9
		5+	8	128	4.9	20.6	2.0
K6	1.8.63	1+	15	43	2.1	1.0	—
K7	14.7.66	3+	18	84	4.9	6.5	1.3
		4+	12	96	7.6	9.4	2.1
KT1	29.7.63	1+	24	46	2.3	1.2	—
		2+	106	75	5.4	4.6	1.2
		3+	16	110	6.0	14.9	3.6
KT2	19.7.66	1+	30	37	3.8	0.6	—
		2+	26	62	3.6	2.8	0.3
		3+	31	86	8.1	7.4	2.1
KT3	19.7.66	4+	7	102	9.2	10.7	3.2
KT4	20.7.66	4+	7	106	8.6	13.7	3.1
KT5	30.7.63	1+	17	45	2.3	1.0	—
		2+	23	78	6.5	5.1	1.3

later than K7 was taken in 1966. The samples indicate a daily increment for 0+ char of 0.44 mm and a daily increment for 1+ char of 0.5 mm. These figures are not intended to be accurate but merely to show the differences between years. Meteorological records for the two years show

that the mean temperature in July 1963 was about 1°C below normal and in July 1966 about 1°C above normal. If July temperature influences growth during that month the differences between years and indicated daily increments may be minimal.

Table 11. *The age and size of trout in Komagelva and tributaries.*

Sample	Date	Age	Number	Length mm	S.D.	Weight g.	S.D.
K4	18.7.66	2+	10	73	3.5	3.6	1.3
KT1	29.7.63	1+	15	53	4.5	1.9	—
		2+	9	91	6.9	9.8	2.6
KT2	19.7.66	1+	8	47	2.2	1.4	0.1
		2+	16	78	2.5	5.9	0.6
KT3	19.7.66	2+	4	98	9.0	11.3	3.5
		3+	39	119	6.5	20.1	3.5
		4+	16	136	8.5	31.1	5.6
KT4	20.7.66	2+	41	79	12.5	6.2	3.5
		3+	26	109	6.9	16.3	3.4
		4+	17	137	8.9	30.6	6.4

Table 12. *The age and size of char in Komagelva and tributaries.*

Sample	Date	Age	Number	Length mm	S.D.	Weight g.	S.D.
K4	18.7.66	0+	29	31	1.8	0.2	—
		1+	177	61	5.2	2.3	0.4
		2+	20	96	8.0	8.7	1.8
		3+	5	113	11.0	14.8	5.0
K6	1.8.63	0+	120	39	3.1	0.6	—
		1+	356	68	5.2	3.4	0.9
		2+	86	99	7.2	10.5	2.3
		3+	6	122	7.8	20.2	3.5
K7	14.7.66	0+	43	25	2.6	0.2	—
		1+	251	59	4.9	2.1	—
		2+	106	95	7.0	8.2	1.6
K8	15.7.66	1+	6	50	3.3	1.3	—
		2+	5	87	4.4	7.4	1.2
KT1	29.7.63	0+	50	32	2.6	0.5	—
		1+	24	61	5.0	2.4	0.7
KT2	19.7.66	1+	12	63	2.8	2.7	0.4
KT3	19.7.66	0+	5	31	4.2	0.3	—
		1+	53	47	4.0	1.1	0.3
		2+	25	80	—	5.5	1.5
		3+	6	106	6.8	13.3	2.8
		4+	18	141	8.5	31.6	6.0
		5+	4	164	5.4	46.9	6.0
KT5	30.7.63	0+	22	38	2.0	—	—
KT6	14.7.66	1+	49	60	7.0	2.3	0.8
		2+	33	96	9.3	8.9	2.7
		3+	23	120	6.6	17.0	3.2
		4+	9	145	7.7	31.5	6.1
KT7	15.7.66	0+	6	25	2.1	—	—
		1+	58	50	5.5	—	—
		2+	93	82	5.7	—	—
		3+	21	120	9.6	—	—

In an attempt to give a composite picture of growth all samples have been combined and the resulting curves are given in Fig. 6. The lines have been drawn free-hand and because of the differences between samples discussed above there has been no attempt to indicate range of size for any species or age group (this can be obtained from Tables 10, 11 and 12). The curves show the length of the various age groups of salmon, trout and char towards the end of July. At this time trout and salmon fry have not emerged from the gravel and dispersed and none were taken in any of the collections. Char fry emerge and begin growing much earlier and, in consequence, they are larger than equivalent aged salmon and trout. This size advantage is maintained for some years. The salmon parr growth curve is complex and influenced by migration, at the beginning of the fourth or fifth summer, of the fastest growing

fish. This results in the depression in the curve at this point. Very few 5+ or 6+ salmon parr remain in the river. The trout and char curves show no similar evidence of migration.

Data on sex ratios is given in Table 13. For all species and all age groups males and females were found in equal proportions. The samples provided very little information on sexual maturity. Amongst the salmon parr 1 male aged 2+, 12 aged 3+ and 1 aged 5+ were maturing. The youngest male trout maturing was aged 4+ and the youngest female aged 5+. Very few char were maturing, females seemed more advanced than males. There was one maturing female in each of age groups 2+, 3+, 5+ and 6+ and 4 in the 4+ age group. A 4+ female 134 mm 26 g contained 97 eggs 2.7 mm dia. The youngest maturing males, 4, were in age group 3+, there were 6 in age group 4+ and 1 in age group 5+.

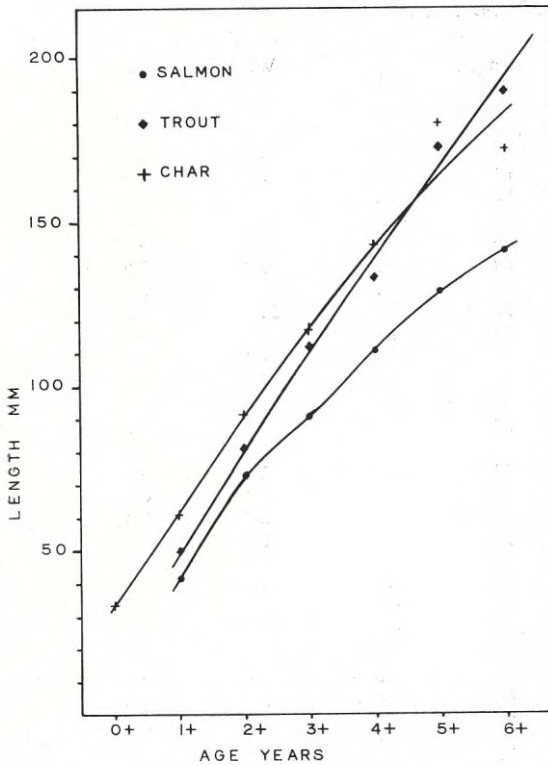


Fig. 6. Composite growth curves for char, salmon parr and trout in Komagelva, approximate date July 25.

Estimates of annual production of fish were made for the samples where this was possible. There were some problems. When fish in the samples had been separated into species and age groups, discretion had to be used in constructing some of the production curves due to small numbers. All estimates err on the conservative side because the method of estimating the numbers of fish in the first two age groups gives numbers which are too low and consequently production is underestimated. The results are given in Table 14. Estimates of annual production differ considerably between samples, but this would be expected because of marked differences between the areas sampled. The sensitivity of the method can be gauged by comparing samples taken in the same place in 1963 and 1966, namely Samples K6 and K7 and KT1 and KT2. In both cases the 1963 samples indicated a higher standing crop and a higher estimate of production. As explained earlier,

Table 13. Sex ratios of salmon, trout and char in Komagelva.

Species	Sex	Age				
		3+	4+	5+	6+	7+
Salmon	Male	110	40	13	—	—
	Female	90	49	13	—	—
Trout	Male	39	25	16	4	1
	Female	40	19	20	3	2
Char	Male	148	26	24	2	—
	Female	129	34	17	2	1

July is a period of rapid growth and higher standing crops in 1963 result from the samples having been taken 18 and 10 calendar days later. Production estimates show even greater change than the biomass, reflecting the rapid change in weight of individuals whose numbers change more slowly, mortality being presumably spread more evenly through the year. Samples K2, K4 and K7 taken in the main river in 1966 within a six day interval show a slight trend towards lower productivity upstream. The sampling sequence K7, K4, K2 would tend to exaggerate this trend while species composition of the samples would tend to reduce it.

Highest production estimates were for the tributary streams. Samples KT1 and KT2 were taken in the lower part of a major tributary and although this area was partly overhung by surrounding willow shrub and offered a considerable amount of cover, the bed was of finer material than in areas KT3 and KT4 in the same tributary. At KT3 and KT4 there was no willow and the valley was open but the stream was narrower and the bed consisted of irregular stones interspersed with gravel which offered good cover for all sizes of fish. Sample area KT6 which shows the highest production estimate was a narrow, deep, meandering channel cut through the main valley deposits of peat and gravel, partly overhung by willow and bank vegetation, offering good cover and maximum edge effects. In addition, only char were present and there were probably minimum losses due to anadromy.

To try to characterize the Komag from these results is not simple because of the variables dis-

Table 14. Estimated biomass and production of salmon, trout and char, Komagelva.

Sample	Estimated Biomass g/100 sq.m.	Annual Production g/100 sq.m.			
		Total	Salmon	Trout	Char
K2	140	103	89	4	10
K4	107	96	30	11	55
K6	101	116	2	—	114
K7	70	90	8	—	82
KT1	95	105	67	22	16
KT2	79	74	36	27	11
KT3	290	216	24	136	56
KT4	195	138	20	112	6
KT6	337	254	—	—	254

cussed. If areas could be sampled in proportion to the amount of each type of area in the system then mean values for standing crop and estimated production would be valid. As it is it seems better to use the separate values as they stand. They do indicate the range of values to be expected for the Komag and they can be used to compare this system with others investigated during this study.

Storelva

This river rises in the Gaisene mountains, the highest in Finnmark and flows northwards to discharge into Storfjord at the head of Laksefjord. It has a drainage area of about 805 sq.km. (BERG, 1964). For the first 10 km. above the sea the river has cut through glacial deposits, has steep banks and flows in shallow braided channels in a flat valley floor. Willow scrub grows in the valley and on islands in the river channel. The bed of the river is unstable consisting of clean round gravel between 2 and 10 cm dia. The current is moderately swift and the river often changes course. Above this the river divides into three branches. The eastern branch is made up of two main tributaries. Badnelusjokka and Vuonjaljokka. These flow in treeless open valleys, have clean fairly unstable stone and gravel beds and contain much meltwater from the high land to the south. The middle branch, Storelva, flows in a flat valley, has a clean, very unstable bottom, and contains very clear water, much of it melt-water from the mountains to the south. The west branch Luobbaljokka rises at a lower altitude and flows through a series of lakes and tarns. Its bed is

stable consisting of rocks, stones and gravel of various sizes. The stones and gravel are dark in colour being covered with a film of epilithic algae, in marked contrast to the clean stones in Storelva and the other tributary. Berg (1964) states that this is the only tributary salmon ascend and that the reason is probably temperature. This tributary contains very fine feeding areas for young salmon whereas in the other branches there is a very clear bottom and little food. The yearly salmon catch is about 1,000 kg, usual weight 5—6 kg and there is a good stock of sea-trout and sea-char in the system. There were no obstacles to fish migration in the parts of the river included in this survey.

The river was sampled in 1963 and more extensive work was carried out in 1966. Fig. 7 shows the locations of the sampling areas and the composition of the fish fauna. Salmon were concentrated in the lower 2 or 3 km of the main river and in Luobbaljokka below Cuolojavrrre. Trout were found mainly in Luobbaljokka and may be the dominant species in the upper reaches of this tributary. Char were found throughout the system and was the only species taken in Storelva above the point where the major tributaries enter. Table 15 gives the dates, areas sampled, numbers of each species taken and the minimum standing crop. It is apparent from the results that some areas are almost barren. Very low standing crops were found in Storelva, except close to the sea, and in Badnelusjokka. This confirms the impression given in the description of the habitat and the statements of BERG (1964).

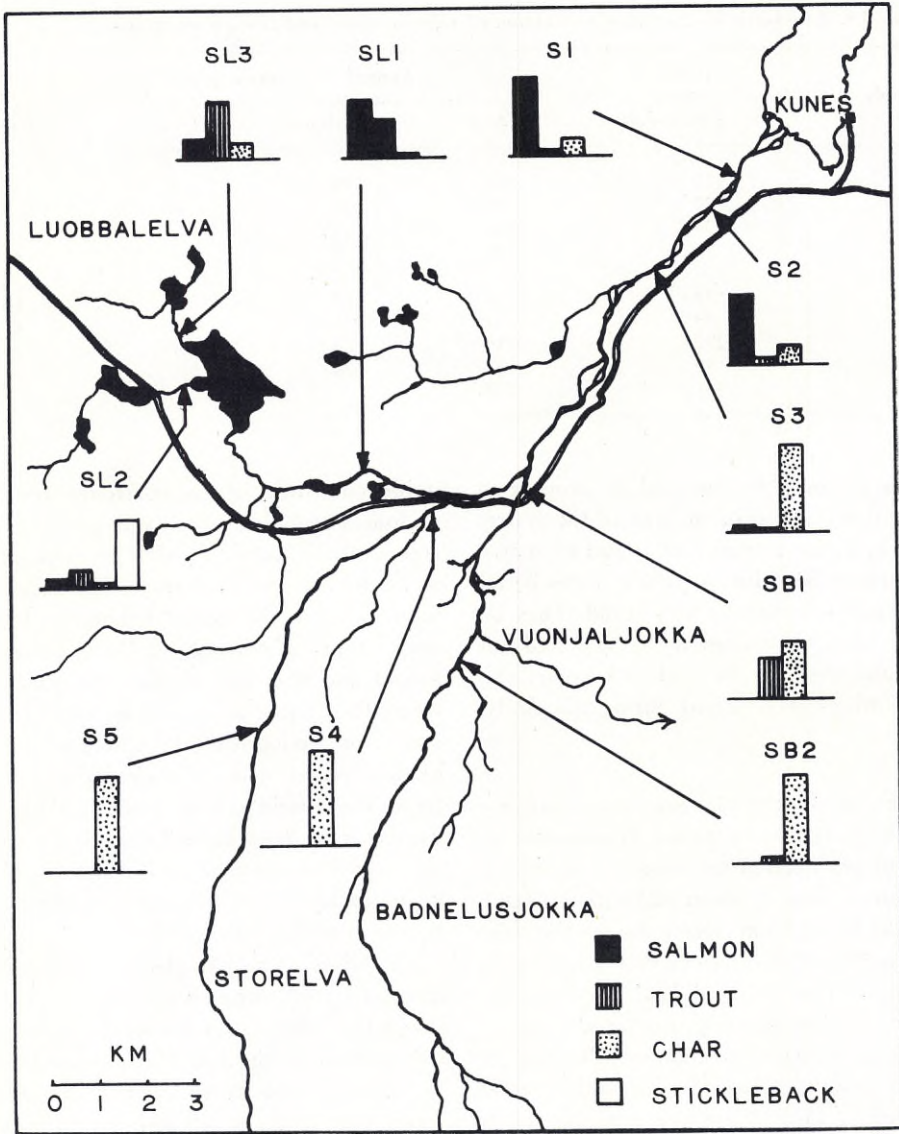


Fig. 7. Sampling sites and the proportions of fish species in collections from Storelva and tributaries.

Details of age and size of salmon parr, are given in Table 16, trout in Table 17, and char in Table 18. Only data from the larger age group samples have been included in the tables. The salmon data comes from the lower part of Storelva and from Luobbaljokka. There is only a slight indication of better growth in the tributary than in the main river. The trout data all comes from Luobbaljokka. Only one fry was taken and

this is included in the table. In contrast char fry are active earlier in the year and many were taken. There is a trend towards slower growth upstream in the char data for 0+ and 1+ fish. The mean lengths of 0+ char were 34 mm, S3; 28 mm, S4; and 27 mm at S5. The mean lengths of 1+ char were 70 mm, S2; 60 mm, S3; 53 mm, S4 and 50 mm at S5. Amongst the older char this trend is not apparent.

Table 15. *Samples, species composition and minimum standing crop, Storelva and tributaries.*

Sample	Date	Temperature °C	Area	Number of Fish by Species				Minimum Standing Crop/100 sq.m.	
				Salmon	Trout	Char	Stickleback	Number	Biomass g.
S1	27.7.66	18.4	660	73	3	18	—	14	76
S2	4.8.63	?	300	67	3	20	—	30	132
S3	25.7.66	17.8	2,220	6	3	92	—	5	21
S4	24.7.66	15.5	3,420	—	—	103	—	3	7
S5	26.7.66	16.0	2,720	—	—	48	—	2	9
SB1	25.7.66	16.0	810	—	8	12	—	3	20
SB2	23.7.66	13.0	816	—	1	15	—	2	13
SL1	24.7.66	18.0	4,640	323	190	7	—	11	105
SL2	26.7.66	20.0	525	20	57	16	245	64	412
SL3	26.7.66	18.5	300	10	29	9	—	16	274
Totals				499	294	340	245		

A composite picture of growth of salmon parr, trout and char in Storelva is given in Fig. 8. Data from all fish in all samples was combined and the curves show the sizes of the three species on about 26 July. The growth curves for char and trout lie parallel with char being an average 3 mm longer in each age group. The growth curve for salmon parr begins parallel but falls away after age 3+ when the fastest growing members of each age group migrate seawards. There is no evidence of a similar effect in the growth data for trout and char.

Data on sex ratios is given in Table 19. For all species in all age groups males and females occur in equal proportions. The samples provide little information on sexual maturity. The numbers of maturing male salmon parr are given in Table

19. A male trout aged 6+ showed evidence of impending maturity, there were 2 females aged 4+, 3 aged 5+ and 1 each aged 6+ and 7+ with ripening ovaries. Only one female char, aged 3+ had enlarging gonads.

Table 20 lists the samples and gives the estimated production of fish. Because of the barren nature of parts of this river system some collections contained few fish. This made estimates of production difficult. Some judicious approximating was necessary in constructing some of the production curves, particularly those for samples SB1 and SB2. Both these came from barren areas and the estimated production is low. In these samples estimated production bears a similar relationship to minimum standing crop as in comparable samples where there was no problem with

 Table 16. *The age and size of salmon parr in Storelva and tributaries.*

Sample	Date	Age	Number	Length mm	S.D.	Weight g.	S.D.
S1	27.7.66	1+	5	54	2.8	1.7	—
		2+	40	73	7.9	4.3	1.5
		3+	27	94	7.7	9.2	2.4
S2	4.8.63	1+	11	50	3.8	1.5	—
		2+	37	70	7.0	4.1	1.1
		3+	16	87	4.9	7.5	1.2
SL1	24.7.66	1+	28	51	3.1	1.7	0.4
		2+	94	77	6.1	5.3	1.3
		3+	148	98	7.1	10.6	2.4
		4+	45	114	7.3	16.5	4.0

Table 17. *The age and size of trout in Storelva and tributaries.*

Sample	Date	Age	Number	Length mm	S.D.	Weight g.	S.D.
SL1	24.7.66	0+	1	25	—	0.3	—
		1+	64	58	3.6	2.3	0.5
		2+	47	79	4.4	5.9	1.0
		3+	48	102	6.8	11.7	3.0
		4+	21	124	8.6	21.9	4.5
SL2	26.7.66	5+	6	149	—	37.3	—
		2+	16	69	7.0	4.1	1.0
		3+	11	101	5.9	12.8	2.1
		4+	14	138	8.9	30.2	6.3
		5+	8	156	7.3	40.0	6.7

Table 18. *The age and size of char in Storelva and tributaries.*

Sample	Date	Age	Number	Length mm	S.D.	Weight g.	S.D.
S2	4.8.63	1+	15	70	5.2	3.0	0.9
S3	25.7.66	0+	24	34	2.7	0.4	—
		1+	32	60	4.0	2.8	0.4
		2+	25	81	7.7	5.3	1.6
		3+	11	103	5.6	10.5	2.1
S4	24.7.66	0+	58	28	2.8	0.2	—
		1+	20	53	4.9	1.7	0.4
		2+	19	84	5.3	5.9	1.0
S5	26.7.66	0+	8	27	1.9	0.2	—
		1+	6	50	2.5	1.4	0.2
		2+	28	77	7.1	5.0	1.4

Table 19. *Sex ratios of salmon parr, trout and char in Storelva.*

Species	Sex	Age					
		2+	3+	4+	5+	6+	7+
Salmon	Total male	92	93	28	5	—	—
	Maturing male	2	22	14	2	—	—
	Female	83	128	22	4	—	—
Trout	Male	29	38	27	6	3	—
	Female	36	27	16	8	2	1
Char	Male	40	13	1	—	—	—
	Female	45	17	1	—	—	—

numbers and it is unlikely the estimates are greatly in error. One sample, SL2, contained a large number of sticklebacks and for these the estimated biomass was taken as equal to the annual production, which is probably an underestimate.

The results show clearly the great differences in fish fauna, standing crop and production in different parts of the Storelva system. Low production is associated with a clean unstable bottom and with meltwater. High production with a stable

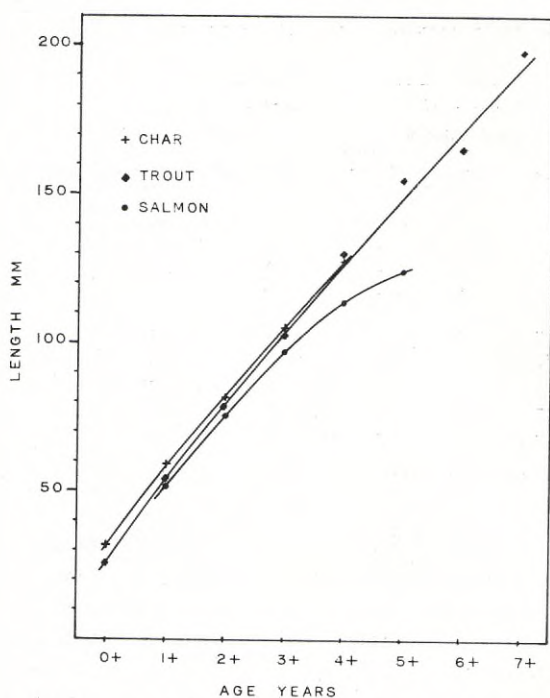


Fig 8. Composite growth curves for char, salmon parr, and trout in Storelva and tributaries, approximate date July 26.

bottom in the tributary with many lakes. In the lower few kilometers of the main river production is again moderately high. Taken as a whole this must be considered an unproductive river system.

Russelva and Ravddulelva

Russelva has its source in the Garddevarre and Davrebrassa highlands between 500 and 600 m above sea level. For the first 16–18 km of its course it flows in a SW direction before turning abruptly NW as it enters a broad U-shaped valley for the remaining 14 km to the sea. This valley supports a birch forest except near the sea. About 2 km from the sea Ravddulelva enters from the NE. It flows in a deep valley, which contains few trees, from the Jalggavaras and Garddevarre mountains. BERG (1964) estimates the drainage area of the system to be about 288 sq.km. In the main river the ascent of salmon is greatly obstructed by a fall about 7 km from the sea. Similarly about 7 km from the sea a gorge and fall prevents anadromous fish ascending Ravddulelva. In 1964 Berg wrote that the stock of salmon in this system was small because of excessive fishing. Most salmon ascend the main river, a few enter the lower reaches of Ravddulelva but this tributary contains mostly sea-char and sea-trout.

The water in Russelva is clear, and in the lower reaches, where sampling was done, there is a stable bottom of stones and gravel. There is some braiding of the main channel and some excellent sites for sampling were available. Ravddulelva contains clear water and has a stable bottom. In the lower 4 km the bottom is small gravel stabilized by larger irregular shaped rocks. Above this there is less gravel and the bottom is com-

Table 20. Estimated biomass and production of salmon, trout, char and sticklebacks, Storelva and tributaries.

Sample	Estimated Biomass g/100 sq.m.	Annual Production g/100 sq.m.				
		Total	Salmon	Trout	Char	Stickleback
S1	154	119	103	10	6	—
S2	209	183	126	3	54	—
S3	34	26	6	2	18	—
S4	9	10	—	—	10	—
S5	14	13	—	—	13	—
SB1	30	16	—	10	6	—
SB2	20	17	—	3	14	—
SL1	197	124	81	42	1	—
SL2	685	376	61	236	11	68
SL3	408	245	72	164	9	—

Table 21. Samples, species composition and minimum standing crop, Russelva and Ravddulelva.

Sample	Date	Temperature °C	Area sq.m.	Number of Fish by Species			Minimum Standing Crop/100 sq.m.	
				Salmon	Trout	Char	Number	biomass g.
Rus 1	3.8.66	19.8	1,300	62	18	12	7	136
Rus 2	3.8.66	19.4	889	122	17	—	16	153
Rus 3	3.8.66	19.8	158	39	5	—	28	291
Rus 4	2.8.66	17.0	800	2	66	—	9	131
Rav 1	6.8.63	—	1,600	47	19	8	5	85
Rav 2	29.7.66	12.2	2,610	132	32	36	8	53
Rav 3	1.8.66	15.5	1,504	63	7	13	6	49
Rav 4	30.7.66	11.8	1,595	—	36	—	2	20
Totals				467	200	57		

posed of square, flat and irregular stones and offers excellent cover for fish. This resulted in the low recovery rate in sample Rav4 (Table 1) in which only 53 % of the marked fish were subsequently recovered.

Details of the samples and the minimum standing crop of fish are given in Table 21. Temperatures when samples were taken indicate that Ravddulelva is colder than Russelva, which may account for the char being concentrated there. Standing crops of fish were lower in Ravddulelva than in Russelva. Locations of sampling sites and species composition of the fish fauna is shown in Fig. 9. The distribution of fish was in accord with the statement of Berg recorded earlier. A surprise in the results was the absence of char in samples taken above the falls. Unfortunately only one sample was taken above the falls in each branch and neither branch was sampled near the headwaters. If char are indeed absent from the upper reaches of this system it would be interesting to know why. This is the only system examined in north Norway where this situation appears to occur.

Analysis of age and size of fish in the samples is given in Table 22 salmon parr, Table 23 trout and Table 24 char. Only the largest age-group samples have been included in the Tables. The results from Russelva include data on 7 salmon fry taken 3 August in sample Rus 3. This was the earliest date salmon fry were encountered in any of the north Norwegian samples. The fry were 28 mm long, 4 mm shorter than char fry taken 6 August in sample Rav 1. The results from Ravddulelva for salmon parr aged 3+ are rather variable. Samples Rav 1 and Rav 2 taken in the same place contained a large stock of big

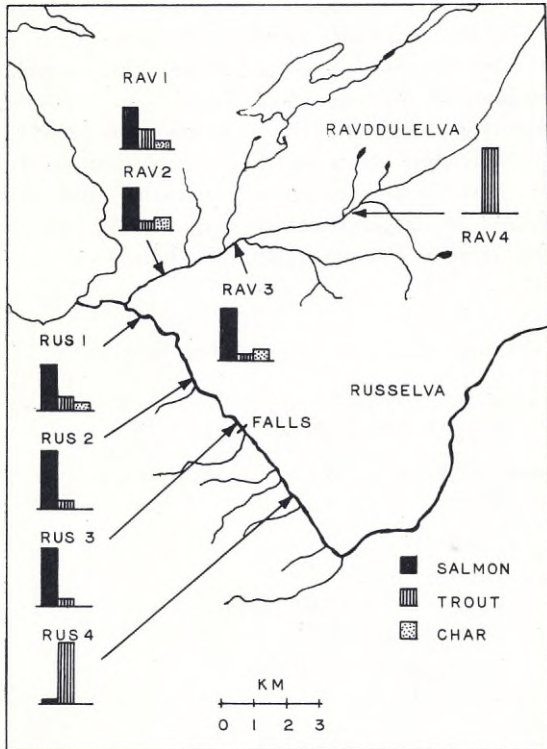


Fig. 9. Sampling sites and proportions of fish species in collections from Russelva and Ravddulelva.

Table 22. The age and size of salmon parr in Russelva and Ravddulelva.

Sample	Date	Age	Number	Length mm	S.D.	Weight g.	S.D.
Rus 1	3.8.66	2+	16	86	6.3	7.7	1.6
		3+	29	104	6.8	13.5	3.5
		4+	11	123	8.9	22.4	5.0
Rus 2	3.8.66	1+	12	53	3.3	1.7	0.3
		2+	41	72	5.3	4.2	1.1
		3+	25	94	4.6	9.4	1.2
		4+	22	114	6.4	16.4	3.2
		5+	19	122	4.7	19.7	2.0
Rus 3	3.8.66	0+	7	28	1.3	0.2	—
		3+	9	92	4.8	9.1	1.8
		4+	10	109	3.9	14.9	2.3
Rav 1	6.8.63	3+	42	117	7.8	18.6	4.0
Rav 2	29.7.66	2+	72	75	6.2	4.5	1.2
		3+	44	87	7.3	6.9	1.6
		4+	7	104	13.5	11.5	4.4
Rav 3	1.8.66	2+	25	79	5.3	5.3	1.1
		3+	22	101	4.4	11.3	1.2

Table 23. The age and size of trout in Russelva and Ravddulelva.

Sample	Date	Age	Number	Length mm	S.D.	Weight g.	S.D.
Rus 4	2.8.66	1+	27	61	4.9	2.5	0.6
		2+	10	89	7.6	8.8	2.8
		3+	12	118	7.2	18.6	3.2
		4+	12	138	11.3	29.3	6.9
Rav 2	29.7.66	1+	12	66	3.3	3.0	0.6
		3+	12	127	5.3	22.7	3.0
Rav 4	30.7.66	2+	30	77	4.9	5.3	1.1

Table 24. The age and size of char in Ravddulelva.

Sample	Date	Age	Number	Length mm	S.D.	Weight g.	S.D.
Rav 1	6.8.63	0+	7	32	7.2	0.2	—
Rav 2	2.7.66	1+	26	61	3.0	2.3	0.3
		2+	10	97	7.3	9.0	2.0

3+ parr in 1963 with few other parr and a smaller stock of small 3+ parr in 1966 together with a large number of 2+ parr. The differences are hard to explain. Perhaps they result from large differences in recruitment from year to year in a tributary which few salmon enter, in a system where the salmon stock is depleted. The results for

Russelva show a trend towards smaller parr in any age group in the upstream samples even though the distance involved was less than 5 km. The trout and char data from this system was much more limited and no similar trends or comparisons were possible.

Composite growth curves for the three species

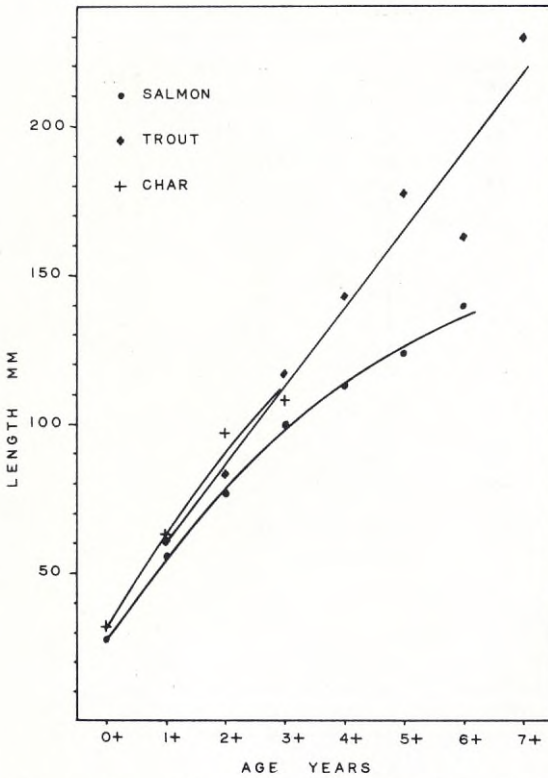


Fig. 10. Composite growth curves for char, salmon parr and trout in Russelva and Ravddulelva, approximate date August 2.

are given in Fig. 10. These curves indicate the size attained by salmon parr, trout and char in the system on about 2 August. Data from all samples was combined to calculate means, curves were drawn freehand. Salmon parr tend to remain in this system longer than in Komagelva or Storelva and the proportion of parr in the 5th and 6th

summers is quite high (Table 25). The growth curve falls away after age 3+ due to migration of the fastest growing parr. The char curve is based on 57 specimens, all from Ravddulelva, of which only 18 were older than age 1+. It shows the size advantage young char have in their first years. Trout were taken in all samples, but slightly more than half the specimens came from above the obstructions. The line joining the means is almost straight and there is no suggestion of similar migratory behaviour to salmon.

Sex ratios and the proportions of sexually mature male salmon parr are given in Table 25. In no group do the sex ratios diverge significantly from a normal 1:1 ratio.

Estimates of production were possible for six samples. Sample Rav 1 was omitted because of the structure of the salmon parr population *i.e.* a large number of 3+ year olds and few others. Sample Rus 3 was omitted because of small numbers and a high proportion of older salmon parr. The results are given in Table 26. Russelva was more productive than Ravddulelva and this would be expected from the nature of the valley through which the lower reaches flow. The lower part of Ravddulelva was more productive than higher up and in Russelva the samples containing a mixed species were more productive than the sample containing almost only trout.

Strupskarelva

Strupskarelva was selected for sampling as an example of a small, glacial stream with quite a steep gradient. The stream originates in the glaciers of the Veidalstind and Lenangstind mountains at over 1100 m. It has a drainage area of about

Table 25. Sex ratios of salmon parr and trout in Russelva and Ravddulelva.

Species	Sex	Age					
		2+	3+	4+	5+	6+	7+
Salmon	Total Males	94	81	29	20	1	—
	Mature Males	1	26	7	11	1	—
	Total Females	70	89	30	10	3	—
Trout	Males	38	19	22	4	2	1
	Females	29	19	17	6	1	—

Table 26. Estimated biomass and production of salmon, trout and char in Russelva and Ravddulelva.

Sample	Estimated Biomass g/100 sq.m.	Annual Production g/100 sq.m.			
		Total	Salmon	Trout	Char
Rus 1	178	118	65	40	13
Rus 2	198	143	133	10	—
Rus 4	158	99	—	99	—
Rav 2	66	80	36	10	34
Rav 3	64	39	29	5	5
Rav 4	49	48	—	48	—

Table 27. Samples, species composition and minimum standing crop, Strupskarelva.

Sample	Date	Area sp.m.	Temperature °C	Numbers of Fish by species		Minimum Standing Crop/100 sq.m.	
				Trout	Char	Number	Biomass g.
St 1	11.8.66	140	12.5	16	1	12	114
St 2	11.8.66	300	12.6	59	7	22	238
St 3	9.8.66	236	12.2	3	17	9	93
St 4	10.8.66	1,050	11.8	6	2	1	6
St 5	10.8.66	300	9.8	—	5	2	6

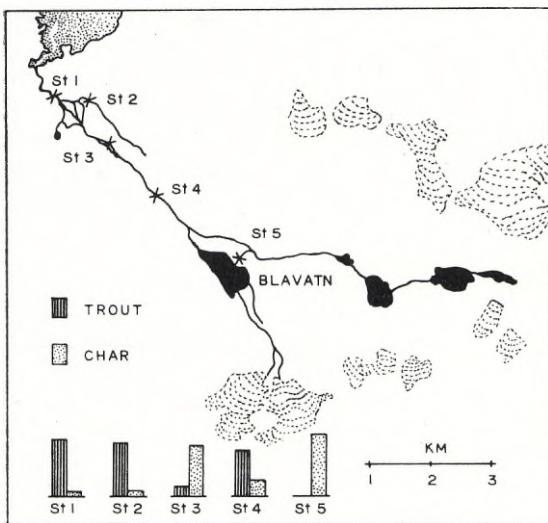


Fig. 11. Sampling sites and proportions of fish species in collections from Strupskarelva, approximate date August 10.

38 sq.km. and is about 10 km long. In the 5 km from the sea to Blåvatnet, a corrie lake 185 m above sea level, there are no falls. The headwater lakes contain glacial water which is very turquoise in colour. The stream bed is of rounded stones and somewhat unstable. Stones at the edge support a film of epilithic algae, over most of the bed they are clean. The water is slightly turbid. In the upper reaches quantitative sampling was impossible as the stream runs under and between large rocks and is partly concealed.

Figure 11 shows the location of sampling areas and the proportions of trout and char taken in each area. Table 27 gives details of the areas sampled, number of fish taken and minimum standing crops. The numbers and biomass are too low in samples St 4 and St 5 because there the stream was unsuitable for sampling. The proportion of char in the samples tended to increase upstream and char may be the only species in

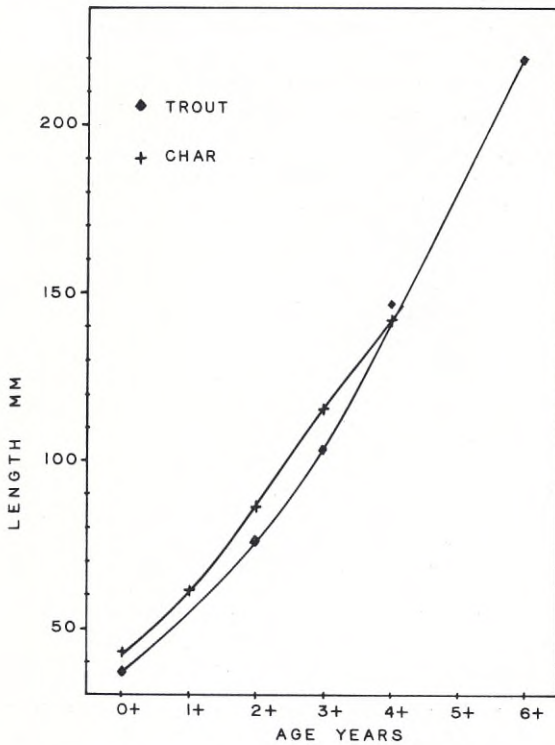


Fig. 12. Composite growth curves for char and trout in Strupskarelva, approximate date August 10.

the higher reaches. Trout were concentrated in the lower parts and in a tributary stream (St2) which originates from small ponds in a peat moor and was warmer than the main stream. Some trout however penetrate far upstream as 6 of the 8 fish taken in St4 were trout.

The numbers of fish in all samples was too low to detect any differences in growth within the

system and all data has been combined to give composite growth curves in Fig. 12. These show the sizes attained by trout and char in the system about 10 August. Sex ratios were equal in all age groups for both species.

Fish production in a stream like this is difficult to estimate. Two samples, St 3 in the main stream and St 2 in a tributary gave estimates of production of 137 g/100 sq.m. and 312 g/100 sq.m. respectively. These values are surprisingly high but these were the only samples containing enough fish to allow estimation of production. Most areas in the main stream will produce less and in the upper reaches production may be very low.

Breivikelva

BERG (1946) estimates the drainage area as about 168 sq.km. and the length about 30 km. The lower reaches of the river are slow and meandering with a bed of soft grey clay overlain by sand and a thin veneer of gravel. The river contains much melt-water and the water in the lower reaches is turbid with eroded clay particles. The tributary streams are clear, cold and swift with beds of rock, stone and gravel. The river supports a small run of salmon and a stock of sea trout and sea char.

Attempts to sample the fish fauna of this system were severely hampered by lack of suitable sampling areas, scarcity of fish and poor weather in 1966 which resulted in rapidly rising water levels. As a result the information obtained was limited. Table 28 summarizes the data from six samples taken in 1963 and 1966. Minimum standing crops by weight were low or very low, where high

Table 28. Samples, species composition and minimum standing crop, *Breivikelva*.

River Distance Above Sea km	Date	Area Sampled sq.m.	Temperature °C	Numbers of Fish by Species				Minimum Standing Crop/100 sq.m.	
				Salmon	Trout	Char	Stickleback	Number	Biomass g.
4	10.8.63	445	14	10	4	1	21	8	49
6.5	15.8.66	1,000	9.5	—	—	4	—	0.4	0.4
20	10.8.63	715	11.8	—	—	195	—	27	22
20	17.8.66	715	8.5	1	—	92	—	13	25
25	18.8.66	273	10.0	1	—	8	—	3	19
Trib.									
20	18.8.66	840	8.1	3	1	176	—	21	100

Table 29. The length of salmon parr and char in Breivikelva about 15 August.

Age	Salmon Parr		Char	
	Number	Mean Length mm	Number	Mean Length mm
0+	1	36	423	38
1+	3	74	29	74
2+	1	99	7	105
3+	8	109	6	130
4+	2	124	6	150
5+	—	—	3	174
6+	—	—	1	209

densities occurred char fry made up the numbers. This result was expected from the unproductive appearance of the sampling areas which offered poor cover. The most productive sample was taken in the lower reaches of Bruelva, a precipitous tributary stream containing mainly char. Here the bottom was stony and offered good cover. The sample contained more larger char than other samples, but still, 147 out of 176 char taken were fry. In the sample 10 out of 12 males aged 3+ or more were maturing sexually; 1 out of 2 females aged 3+ or more was maturing.

Table 29 summarizes the data on age and length. Data from all samples has been combined but even so only 14 salmon parr were taken and only 52 char beyond the fry stage. The data suggests that the growth rate of both salmon parr and char is better in this system than in those examined further north and east.

Only three samples were suitable for estimation of fish production, the others contained too few fish. Two estimates in the main river from the

same area, 20 km above the sea, gave estimates of production of 66 g per 100 sq.m. in 1963 and 56 g per 100 sq.m. in 1966. An estimate from the lower 210 m of Bruelva which discharges into Breivikelva just above this point gave a value of 97 g per 100 sq.m. Production estimates for the other samples, were it possible to calculate them, would be similar or much lower as indicated by the minimum standing crop data in Table 28. Breivikelva appears to be an unproductive river, much of which is unsuitable for sampling by the methods employed in this study.

Leirskarelva

Leirskarelva, a tributary of Røssaga was selected for study for two reasons. It was to be modified by hydro-electric development and it contained very turbid water which originated from the large Okstind icefield. Discharge and turbidity vary with temperature. Warm weather causes increased turbidity and flooding with cold melt water from the glaciers. An inspection of the river in summer would lead to the conclusion it must be very unproductive. Visibility is restricted to a few cm and the bottom is blanketed in fine silt. Conditions appear so bad it is hard to believe fish would live in the main stream. Tributaries in the lower valley contain clear water but fall precipitously down the valley sides. At the head of the main valley where the river turns north-south is a series of waterfalls several 100 m high. The turbid water all enters the system from the south in Mørkelva. Above this the river is clear. The river bed is of stones, rock and gravel. There are farms in the lower valley and some forest. Agriculture is mainly hay pro-

Table 30. Samples, species composition and minimum standing crop, Leirskarelva.

Sample	Date	Temperature °C	Area sq.m	Numbers of Fish by Species			Minimum Standing Crop/100 sq.m.	
				Salmon	Trout	Char	Number	Biomass g.
L1	24.8.66	7.8	2,100	137	295	5	21	136
L2	12.8.63	11.3	660	—	178	—	27	201
L3	23.8.66	12.0	330	1	259	1	79	147
L4	24.8.66	9.0	950	3	325	1	35	223
L5	25.8.66	—	—	—	—	25	—	—
LT1	24.8.66	10.4	368	18	100	—	32	536

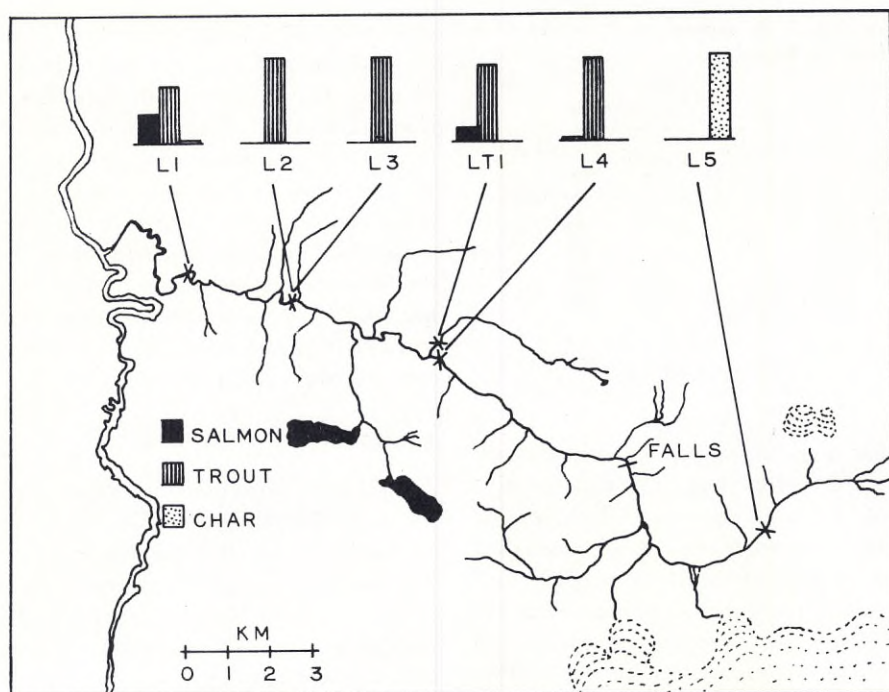


Fig. 13. Sampling sites and the proportions of fish species in collections from Leirskarelva.

duction for the support of dairy cattle. BERG (1964) reports salmon taken in Leirskarelva are usually less than 13 kg and most ascend in the autumn. The annual yield is about 800 kg. There is a large stock of sea trout of less than 1 kg.

The river was sampled in 1963 and again in 1966. Details of the samples, the numbers of each species taken and the minimum standing crop are given in Table 30. The river provided some very good areas for sampling and surprisingly, in spite of bad visibility and much potential cover, recovery of marked fish was good (see Table 1). Under the conditions in Leirskarelva a larger proportion of fish were recovered in the barrier net

than was usual. Fig. 13 shows the sampling locations and the composition of the fish fauna in each. Salmon parr are concentrated in the first few km of the river and a few in the lower parts of tributaries. This is obviously a trout river and trout predominate in all samples below the waterfalls. Above the waterfalls there are only char. A few char occur in other parts of the system but the numbers taken in the samples were negligible.

Only one sample contained enough salmon parr to provide information on age and size. Details are given in Table 31. A single fry was taken but larger numbers of older fish. There was some

Table 31. *The age and size of salmon parr in Leirskarelva.*

Sample	Date	Age	Number	Mean Length mm	S.D.	Mean Weight g.	S.D.
L1	24.8.66	0+	1	31	—	0.4	—
		1+	17	60	9.5	2.5	1.0
		2+	103	82	8.8	6.0	2.0
		3+	14	105	8.7	12.5	4.0

Table 32. The age and size of trout in Leirskarelva.

Sample	Date	Age	Number	Mean Length mm	S.D.	Mean Weight g.	S.D.
L1	24.8.66	0+	48	32	3.9	0.33	—
		1+	82	63	5.8	2.7	0.5
		2+	112	85	8.9	7.0	2.5
		3+	45	112	11.2	16.8	4.8
L2	12.8.63	0+	32	29	2.2	0.25	—
		1+	41	56	6.9	2.6	0.8
		2+	43	82	10.5	7.0	2.8
		3+	54	103	12.0	13.3	4.6
L3	23.8.66	0+	205	31	3.6	0.24	—
		1+	24	62	5.8	2.8	0.8
		2+	15	88	6.5	7.8	1.9
		3+	13	106	9.3	14.3	3.9
L4	25.8.66	0+	132	30	2.8	0.28	—
		1+	68	56	4.5	1.9	0.5
		2+	74	88	8.2	8.0	2.6
		3+	37	116	11.5	19.5	6.1
LT1	24.8.66	1+	18	59	4.8	2.1	0.6
		2+	37	90	10.3	9.0	4.2
		3+	25	116	9.2	20.0	4.0

difficulty assigning ages to some fish and where there was doubt otoliths as well as scales were examined. Similar problems were encountered interpreting trout scales and otoliths were used instead for age determination. Details of the age and size of trout are given in Table 32. There were no apparent differences in growth in different parts of the main river or in the tributary sampled.

Growth curves for salmon parr, trout and char are given in Fig. 14. The means were derived by combining data from all samples. The curves for salmon parr and trout coincide for the first three years, then the salmon curve falls away as the faster growing parr migrate. The char curve is derived almost entirely from the 25 char taken in sample L5. This was taken beyond the region influenced by glacial silt, about 750 m above the lower valley, and growth was better. The difference between the char and trout curves gives some idea of the depressing effects of the turbid water on growth.

Data on sex ratios indicated no significant difference from equality in any age group for any species. Two male salmon parr aged 5+ and 6+ were sexually mature. The youngest male trout maturing was a male age 2+, there were 6 out of 82 3+ males maturing, 4 out of 14

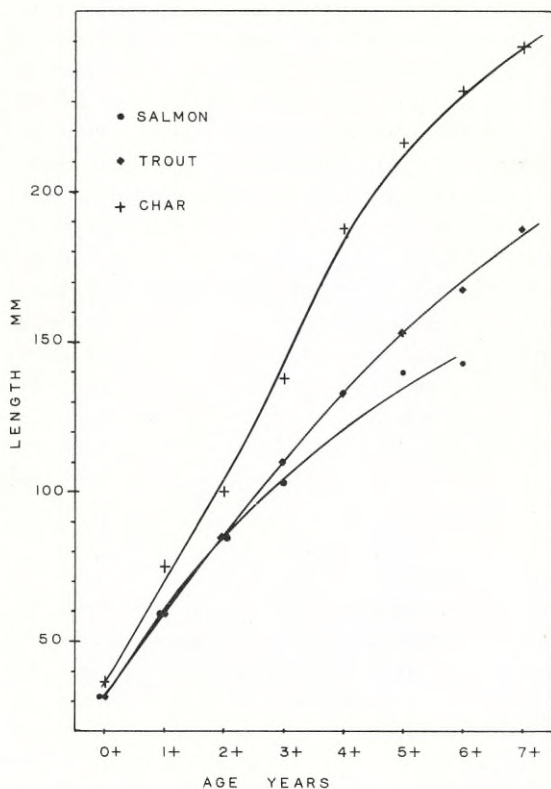


Fig. 14. Composite growth curves for char, salmon parr and trout in Leirskarelva, approximate date August 23.

Table 33. *Estimated biomass and production of salmon, trout and char in Leirskarelva.*

Sample	Estimated Biomass g/100 sq.m.	Annual Production g/100 sq.m.			
		Total	Salmon	Trout	Char
L1	136	190	71	117	2
L2	201	215	—	215	—
L3	147	211	3	205	3
L4	223	259	1	258	<1
LT1	536	614	49	565	—

4+ males, and all the older males maturing. No sexually mature females were included in the samples. Male char matured at age 3+. Four females were mature. Their length, age and egg counts were as follows: 216 mm, 5+, 442 eggs; 241 mm, 6+, 528 eggs; 245 mm, 7+, 400 eggs; and 268 mm, 7+, 475 eggs.

Five samples were suitable for estimating fish production. The results are given in Table 33. Production was estimated at slightly better than 200 g per 100 sq.m. per year in the main river. It was about three times this in the lower part of Finbakelva, the only tributary sampled. Trout account for most of the production except in the lower sample, L1, where salmon contribute about 38 % of the total. The only other sample where salmon contribute much is the tributary LT1 where salmon account for 6 % of the total. The salmon values are affected by migration, the trout situation is less clear, but in view of the river being known to support a large stock of sea trout there must be some losses due to migration from the trout population also.

IV. DISCUSSION

The purpose of this work was to provide an insight into the nature of the populations of salmonids inhabiting some north Norwegian rivers and streams. The scope was extensive and in these latitudes the field season is brief and work must be accomplished in a short time when weather and other conditions permit. In 1966 the weather was exceptionally favourable and this allowed much to be accomplished. The study includes some of the most northerly watersheds in Europe and some

rivers farther south that are greatly influenced by melt-water from glaciers. The results are of interest in showing how salmonid species respond to these conditions and to show approximately what levels of production can be realized.

In evaluating the results a number of points need to be considered. The most serious question is, do samples obtained by the methods employed adequately represent the populations present? Those samples taken in tributary streams and small rivers where the whole width of a typical section was taken are undoubtedly representative. This applies to 15 of the 40 samples from which production was estimated. Other samples were taken in branches of larger rivers. Here every attempt was made to select areas that were like the main river, that contained enough deep water to provide habitat for larger fish and that had similar flow and bottom materials to the main river. Northern rivers, particularly glacial rivers with braided channels offer many good sample sites. The 7 samples taken in Storelva and its tributary Badnelusjokka were from a braided watercourse and must have been typical of the stock in the river. In Komag, Russelva, Ravddul-elva and Leirskarelva the sample areas were noted as being good or very good in respect to similarity to the main river. In Breivikelva and Strupskarelva they were poor and probably did not provide good samples of the river population. Even where sample areas were noted as very good the question remains as to whether older, larger and more aggressive fish occupy these areas or only the widest and deepest parts of the main river, thus biasing samples in favour of younger fish. This question cannot be resolved but the relative scarcity of large fish suggests such fish may be under-

represented. This would result in an underestimate of biomass in samples from the main rivers. Estimates of production would be less affected because the greatest contributions to production in these populations are made by fish in their third through fifth summers. In addition, areas not occupied by large fish will presumably be utilized by small fish.

A problem of a different sort is posed by the anadromous habits of the salmon, trout and char. The salmon are anadromous and all the major rivers examined are reported to contain populations of sea trout and sea char. No information was available about the small rivers and streams but the inference is they contain only resident trout and char populations. Several large trout and char were excluded from samples because they had returned from the sea. Loss of biomass as a result of migration to the sea cannot be estimated. As far as can be judged errors resulting from this would be small for trout and char, the growth curves Figs. 6, 8, 10 and 12 support this. Other support comes from samples taken in Russelva and Ravddulelva, above falls where losses due to migration to sea are unlikely. In these, estimated production was lower than in areas downstream. Losses from the salmon population are inevitable and production is underestimated as a result of migration. No attempt has been made to compensate for this.

Another complication arises from changes that occur in the population during the brief summer growing season. Ideally, for accurate assessments of production, estimates of population density and mean weight for each age group of each species of fish should be obtained at intervals throughout the year (CHAPMAN 1967, 1968). Under the circumstances that this work was conducted this was obviously not possible and at the time the samples were taken the fish were rapidly increasing in length and weight. It is not known whether this was accompanied by a similar increase in mortality or whether mortality was distributed differently throughout the year. The present data does not provide much information on the question. There was an indication in the data obtained from the small streams near Komagvaer that numbers of young fish change rapidly during the summer. Figure 4 illustrates the situation. In samples taken

early in July the 1+ age group was numerous and well defined. By August when the fry had emerged the numbers of 1+ age group fish had diminished greatly in proportion to the number of older fish in the population. If mortality was spread more evenly through the year it would result in higher estimates of production later in the growing season. This is because weight is increasing more rapidly than numbers are decreasing. There were indications of this effect in the results for the streams near Komagvaer and Komag and this has already been discussed. An exception was samples L2 and L3 taken in the same place in Leirskarelva. Here water levels were changing fast and the area sampled in 1966 was only half what it was in 1963, although the day before it had been the same. This must have a considerable effect on the fish population and the two samples are not easily compared.

In relating biomass to production the age structure of the population has an influence. Populations with a high number of young and few older fish have a higher production in relation to their biomass than populations with lower mortality rates. This is because the proportion of production removed by mortality is much greater in such populations than that remaining as biomass. For this reason it is not possible to give a factor by which the minimum standing or the estimated standing crop should be adjusted to give the estimated production.

During the field work and subsequent analysis of the results it became evident that a number of factors affect the biomass and estimated production of fish in a sample area. The type of bottom is most important. A bottom of sand or silt is unproductive and affords little cover for larger fish. In such areas there may be a high proportion of fry but standing crops and estimated production are low. Breivikelva was an example of this. An unstable bottom of clean rounded gravel and stones such as occurs in Storelva is perhaps even less productive and, except near the sea and in the one tributary of a very different nature, fish were very scarce in this system. A mixture of coarse and fine gravel stabilized with some larger stones, a coarse gravel and stoney bottom or a stoney bottom appear to offer the best possibilities for fish production. Cover such as can be provided

by under-cutting of peat banks, roots and branches is also good. A film of epilithic algae on the bottom indicates stability and a higher level of production. Edge effects are important and narrow streams support a greater biomass of fish than wider ones. This results in tributary streams being more productive than branches of the main river. Very small streams such as those near Komagvaer and the tributary of Strupskarelva, which are partly overhung by surrounding vegetation, can be very productive. In branches of larger rivers any relationship between width and estimated production is obscured by other factors. Side effects may be less important here anyway because the banks are often stoney and exposed at summer water levels.

Of interest in the results was the way the fish species were distributed. In larger rivers the general pattern of salmon in the lower reaches, trout upstream or in the warmer tributaries, and char in the headwaters and cold tributaries, was followed with only one exception. Char appeared to be absent in the upper reaches of the Russelva, Ravddulelva system. In smaller rivers and streams only char were found unless they were warm enough to allow trout to establish themselves. The result of this spatial distribution was that most samples contained either only one species or were predominantly one species. In 25 of the 40 samples from which production was estimated one species was responsible for all or effectively all the production, in 11, two species contributed, although one usually predominated, and in 4, three species were involved. Examination of Tables 14, 20, 26 and 33 reveals only 8 samples in which two species each contributed at least 30 % to the total production. The sample in which production was most nearly shared between the three salmonid species was sample K4 in which salmon contributed 30 %, trout 12 % and char 55 % of the total production. It was apparent that, in summer, salmon, trout and char were effectively segregated in these northern watersheds. Reasons for this cannot be deduced from this work, except that, the observed distribution and a few measurements suggest that temperature regime may be important. Other work, particularly the detailed studies of Nilsson, summarized in NILSSON (1963, 1965) shows that amongst other things a slight preference for par-

ticular food items leads to segregation of trout and char in north Swedish lakes. This was most marked when food was least plentiful, as in regulated reservoirs or in late summer. On the other hand KALLEBERG (1958) stresses the importance of aggression and territorial behaviour in stream salmonids. His stream tank observations showed trout tend to be more aggressive than salmon parr. This explains the distribution observed by LINDROTH (1955) in a large Swedish river. Trout occupied shallow areas along the river margins and salmon parr deeper water, a pattern of distribution that appears to differ from that occurring in smaller north Norwegian rivers.

A most unexpected result was the similarity of the growth in all systems. With allowance for the dates on which samples were taken a single curve could describe the growth of char in the tiny streams near Komagvaer, in Langvikelva, Troldelva, Komagelva, Storelva, Ravddulelva, Strupskarelva, Breivikelva and Leirskarelva. The same applies to the salmon and trout. Comparison of figures 6, 8, 10, 12 and 14 shows this clearly. The char appear to have a slight edge in these northern streams because the fry emerge and begin growing earlier than either salmon or trout fry. How much earlier is uncertain. Char fry were taken in samples from the beginning of July but not in quantity until after the middle of the month. Trout fry were not taken in quantity before the sampling in Leirskarelva towards the end of August about a month later and although salmon fry were taken in Russelva at the beginning of August they were never encountered in quantity. Growth curves for the three species are parallel at first but the salmon curve falls away as a result of migration of the fastest growing parr.

Sex ratios for all species, in all age groups, were even which was surprising. Generally older salmon parr are predominantly males which become sexually mature and therefore remain longer in the river than the females. The numbers of older salmon parr taken were quite small and this may account for the results observed.

The greatest contrasts in the results were in biomass and estimated production. Production estimates are summarized in Table 34. Biomass ranged from a low estimated standing crop of between 9 and 34 g/100 sq.m. in parts of Stor-

Table 34. Estimated production g/100 sq.m./year in areas located in north Norwegian rivers and streams.

Watershed	Estimates of Production g/100 sq.m./year
Langvikelva	72
Troldelva	94
Streams by Komagvaer	201, 368
Komagelva	74, 90, 96, 103, 105, 116, 138, 216, 254
Storelva	10, 13, 16, 17, 26, 119, 124, 183, 245, 376
Russelva, Ravddulelva	39, 48, 80, 99, 118, 143
Strupskarelva	137, 312
Breivikelva	56, 66, 97
Leirskarelva	190, 211, 215, 259, 614

elva to values as high as 531 in the small streams near Komagvaer, 685 in a tributary of Storelva and 837 in a tributary of Leirskarelva. Estimated production in the same locations went from a low of between 10 and 26 g/100 sq.m. to highs of 368, 376 and 614. From the lowest to the highest values this is an increase of 50 to 80 times in biomass and 40 to 60 times in production.

The inescapable conclusion to be drawn from the observations on growth, biomass and production is that under the severe conditions existing in these northern and glacier-influenced watersheds growth is reduced to the lowest level compatible with survival. All other adjustments in the population involve changes in density in response to the severity of the conditions. The controlling factor here is undoubtedly food supply although the results cannot show this. ALLEN (1951) in his detailed study of the trout population in the Horokiwi stream in New Zealand came to the conclusion that trout production was largely limited by food supply.

Comparison of the results obtained in north Norway with other published estimates of production shows that in general production is low in these northern waters. In the Horokiwi, trout growth is rapid, the fish average between 180 and 220 mm fork length at the end of the first year and production was estimated at 5,436 g/100 sq.m./year, almost 50 times the average for north Norway. The Horokiwi seems to be much more productive than most streams and CHAPMAN (1967) quotes a series of values which range upwards from 100 g/100 sq.m./year with the median

being about 1,800 g/100 sq.m./year for salmonid production in running waters. LE CREN (1969) provides figures for a series of small streams in England where the dominant species was trout or trout and sculpin. Trout production varied between 300 and 1,200 g/100 sq.m./year but in chalk streams where sculpins were common sculpin production could exceed trout production by 3 or 4 times. On the basis of his own and other data he suggested a maximum level of production for stream salmonids of 1,200 g/100 sq.m./year, about 10 times the average production observed in this study. The highest estimate of production, 614 g/100 sq.m./year in a tributary of Leirskarelva, shows that moderate levels of production may be achieved in small favourable areas in north Norway. GOODNIGHT and BJORN (1971) estimated salmonid production in Big Springs Creek, Idaho, at 1,100 g/100 sq.m./year, a value close to LE CREN's suggested maximum while in the Lemhi River fish production was estimated at 1,250 g/100 sq.m./year about equally divided between salmonids and whitefish. Higher levels of production were reported for a Scottish stream by EGGLESHAW (1970). Over a three year period salmon production ranged from 650 to 1,060 g/100 sq.m./year while trout production in the same period ranged from 1,030 to 1,230 g/100 sq.m./year. The published results show a wide range of variation but almost all values exceed by a considerable amount the estimates for north Norway, a difference which is to be expected considering the latitude, climate and nature of the rivers that were chosen for study. What is now needed is detailed study of production in a single river system to see how growth, mortality and production are distributed throughout the year. The practical aspects of such a study would be extremely difficult because of winter and frequent flood conditions.

Practical Considerations

From a practical standpoint the most useful thing this study can do is attempt to set guidelines for estimating the fish production in other north Norwegian watersheds. The sampling technique employed is not recommended for use by inexperienced people. The danger of extensive fish kills

Table 35. *Habitat adjustment factors for calculating production. Start with 140 g/100 sq.m./year and multiply by appropriate factor for each condition.*

Conditions						
A						
Stream bottom	Unstable clean gravel and stones	Sand and silt	Fine gravel only	Coarse and fine gravel stable	Coarse, fine gravel and stones	Stony bed or much cover
	0.2	0.4	0.8	1.0	1.2	1.4
B						
Width of Stream	less than 3 m	3—5 m	5.5—11 m	more than 11 m		
	2.0	1.1	1.0	0.9		
C						
Valley (omit if stream is less than 3 m	Open tree-less	Stunted forest	Forest	Some Agriculture	Agriculture	
	0.7	0.9	1.0	1.1	1.3	
D						
Predominant Species	Char	Salmon	Trout			
	0.8	1.0	1.2			
E						
Water Quality	Very Turbid Glacier Water Siltling	Slightly Turbid Glacier Water		Clear Water		
	0.4	0.7		1.0		
F						
Growing Season	Finnmark	Troms		N. Nordland	S. Nordland	
	0.9	1.0		1.2	1.4	
Any adverse factor, e.g very steep gradient				0.8		

from overdoses of rotenone and improper neutralization are far too great and the technique is too drastic for widespread application. In addition, analysis of samples is time consuming and age determination requires considerable experience to be reliable. In view of these considerations an attempt has been made to develop a simple practical way of estimating production and it is offered here with no apologies.

All that is needed is knowledge of which salmonid species is dominant in an area and some details about the habitat and the surrounding terrain. Production is then calculated from the habitat adjustment factors given in Table 35. These have been derived by trial and error to give results which approximate closely those obtained in the present study. With an additional adjustment for the date of sampling of 0.8 before

20 July and 1.2 after 12 August the agreement between production estimated from field data and that calculated using the table of habitat factors is good. The data is plotted in Figure 15, the diagonal line represents a perfect fit. Exceptions to a good fit are two samples taken near to the sea in Storelva where there is a wide discrepancy. These can be ignored as unusual and resulting from drift from the productive tributary enriching the lower part of Storelva. Another exception is the tributary of Strupskarelva which emerges from the moorland pools, but this is small and unimportant. Apart from this the worst fit is the data for the upper samples from Russelva and Ravddulelva where field estimates of production are much lower than that calculated from habitat factors. The reason for the difference is not known.

The difficulty with Table 35 is that judgement

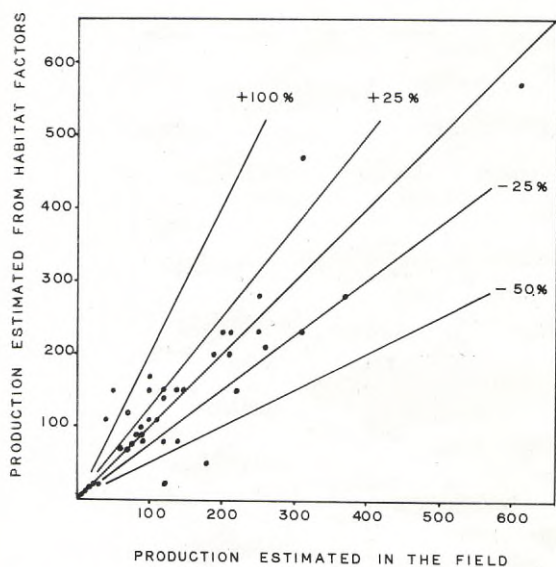


Fig. 15. Comparison between production estimated in the field and that calculated from habitat factors for the same 39 areas.

concerning the conditions will vary somewhat from observer to observer. This can be minimized by defining the subjective categories more precisely.

The stream bed

Unstable, clean gravel and stones: The stones move and roll when walked on, the stream is often changing course, the stones and gravel are round and have no visible film of epilithic algae on the surface, e.g. the conditions in much of Storelva.

Sand and silt: These are particles less than 1 mm dia.

Fine gravel: Small stones often rounded less than 1 cm dia.

Coarse and fine gravel, stable: Stones of varied sizes up to 5 cm dia. These are conglomerated into a stable bottom that does not shift when walked on. Generally the stones are darkened by film of epilithic algae.

Coarse, fine gravel and stones: Similar to above but with some larger stones interspersed which provide more cover for large fish and provide stability.

Stony bed or much cover: The bottom composed mainly of stones more than 5 cm dia. and providing many crevices and much cover for fish. Alternatively, cover can be provided, usually in smaller streams, by roots, undercut banks and fallen trees and other vegetation.

The valley

Open, tree-less: These are areas where only a few stunted trees and shrubs can be seen, e.g. Komag, Ravddulelva.

Stunted forest: This is the forest near the tree-line, small birch trees well spaced and averaging only 4—5 meters high, e.g. Storelva near sea, Russelva.

Forest: Thicker, more continuous forest, usually more than one species of tree, average height more than 5 meters.

Some agriculture: Some farms in the valley in clearings in the forest. Usually only hay grown, e.g. Breivikelva.

Agriculture: Most of the suitable land farmed. Mainly hay and dairy farming, also other crops, e.g. Leirskarelva.

Water quality

Very turbid glacier water, silting: Visibility through the water restricted to 20 cms or less. Silt settling out from the water, e.g. Leirskarelva.

Slightly turbid glacier water: This is the green water carrying glacial silt but not enough to markedly reduce visibility or to settle out, e.g. Strupskarelva.

Clear water: Water not carrying a load of silt and generally not originating from glaciers, e.g. Komag and most rivers.

With these details it is thought that most observers will be able to determine the habitat adjustment factors from Table 35 and calculate production to within $\pm 50\%$ of the probable value. What production means in terms of fish is illustrated in Fig. 16 in which two populations are shown, one with a production of about 100 g/100 sq.m./year and the other with a production of 300 g/100 sq.m./year. These give an impression of the population in terms of numbers and sizes

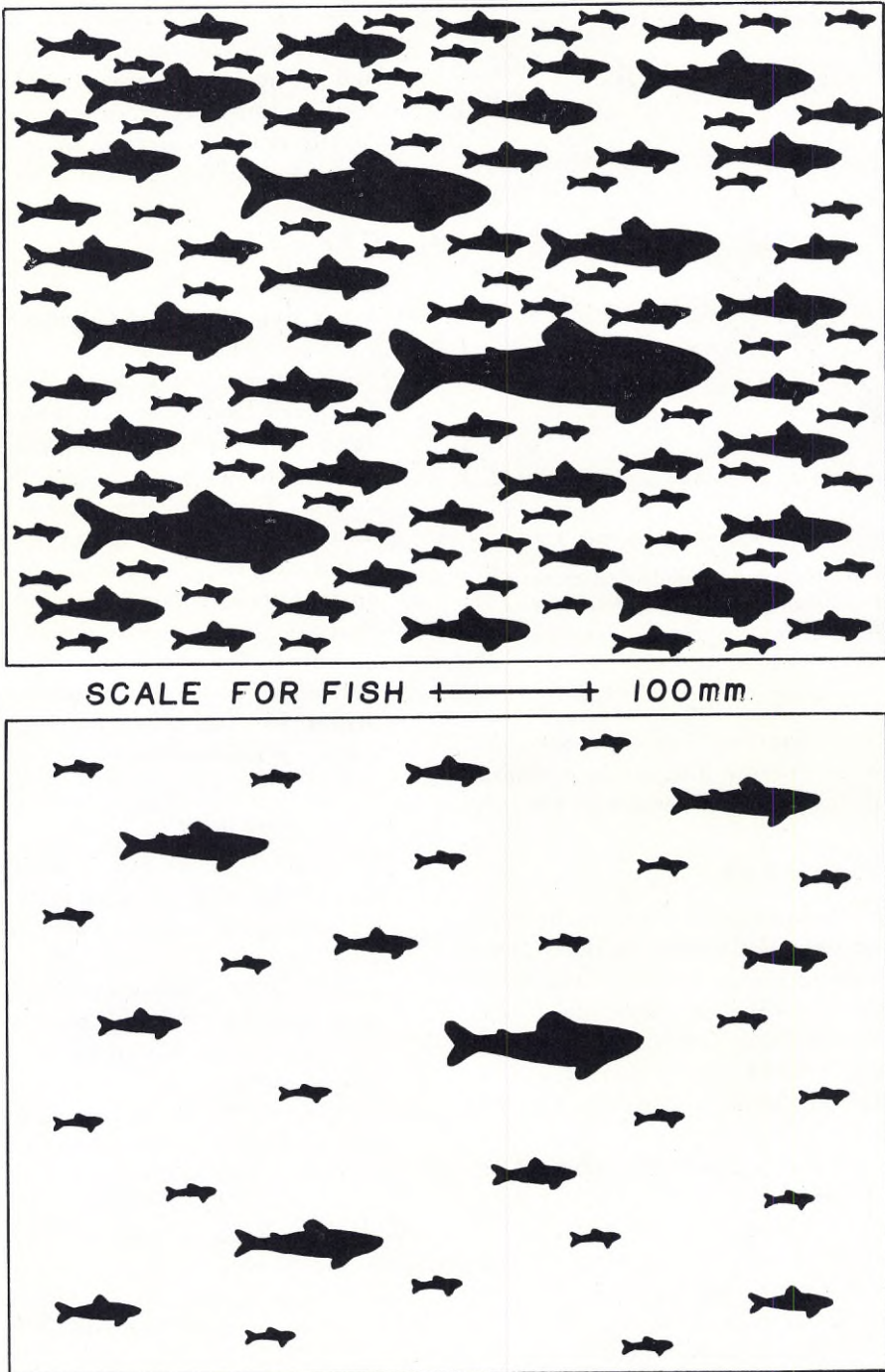


Fig. 16. Fish populations per 100 sq.m. Upper panel — a salmon parr/trout area producing approximately 300 g/100 sq.m./year. Lower panel — a char area

producing approximately 100 g/100 sq.m./year. Age groups identified by size.

of fish in each age group. For predominantly trout populations there will be slightly fewer small fish and a few more large fish. For salmon, because of migration, there are few large fish. It is hoped the last part of this report will enable anyone interested to gain a clear picture of the fish populations inhabiting the rivers and streams of north Norway.

V. SUMMARY

Collections containing over 8,000 specimens of char, salmon parr and trout obtained by use of rotenone in Langvikelva, Troldeleva, Komagelva, Storelva, Russelva, Strupskarelva, Breivikelva and Leirskarelva are described. Species were generally segregated with char occupying headwaters and cold streams, trout warmer tributaries and downstream parts of rivers too small for salmon and salmon the lower reaches of rivers. Growth of all species was similar in all waters. Annual increments averaged 30 mm. Char fry emerged earliest and the slight advantage in size they attain during the first summer was maintained throughout the first 4—6 years of life. Most salmon parr migrate to sea during their fourth or fifth summers. Standing crops were as low as 9 g/100 sq.m. in glacial rivers with unstable beds but can be as high as 800 g/100 sq.m. in narrow favourable streams. Annual estimates of salmonid production ranged from 10 to 614 g/100 sq.m./year with a mean for 39 estimates of 150 g/100 sq.m./year and a median of 116 g/100 sq.m./year. A method for calculating estimated production in north Norway by use of habitat adjustment factors is described.

VI. ACKNOWLEDGMENTS

I would like to express my sincerest thanks to all who helped make this work possible. In particular, Magnus Berg and Peik Bendixen for their guidance and stimulating help in the field and Mrs. Isobel

Mackay for her assistance in analysis of the collections. Financial support was provided by an operating grant from the National Research Council of Canada and summer research stipends from the University of Waterloo.

VII. REFERENCES

- ALLEN, K. R. 1951. The Horokiwi Stream. A study of a trout population. *New Zealand Mar. Dept. Fish. Bull.*, 10: 1—238.
- BERG, M. 1964. Nord-Norske lakseelver. Johan Grundt Tanum Forlag, Oslo. 300 p.
- CHAPMAN, D. W. 1967. Production in Fish populations. p. 1—29. In *The biological basis of freshwater fish production*. Ed. S. D. GERKING. Blackwell Scientific Publications. Oxford and Edinburgh.
- 1968. Production p. 182—196. In *I.B.P. Handbook No. 3. Methods for assessment of fish production in freshwaters*. Ed. W. E. RICKER. Blackwell Scientific Publications. Oxford and Edinburgh.
- EGGLISHAW, H. J. 1970. Production of salmon and trout in a stream in Scotland. *J. Fish. Biol.*, 2(2): 117—136.
- GOODNIGHT, W. M. and T. C. BJORN. 1971. Fish production in two Idaho streams. *Trans. Amer. Fish. Soc.*, 100(4): 769—780.
- KALLEBERG, H. 1958. Observations in a stream tank of territoriality and competition of juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). *Rep. Inst. Freshw. Res. Drottningholm* 39: 55—98.
- LE CREN, E. D. 1969. Estimates of fish populations and production in small streams in England. p. 269—280. In *H. R. MacMillan Lectures in Fisheries. Symposium on salmon and trout in streams*. Ed. T. G. NORTHCOTE. Univ. British Columbia.
- LINDROTH, A. 1955. Distribution, territorial behaviour and movements of sea trout fry in the River Indalsälven. *Rep. Inst. Freshw. Res. Drottningholm* 36: 104—119.
- NILSSON, N.-A. 1963. Interaction between trout and char in Scandinavia. *Trans. Amer. Fish. Soc.* 92(3): 276—285.
- 1965. Food segregation between salmonid species in North Sweden. *Rep. Inst. Freshw. Res. Drottningholm* 46: 58—78.
- NORDENG, H. 1961. On the biology of char (*Salmo alpinus* L.) in Salangen, North Norway. I. Age and spawning frequency determined from scales and otoliths. *Nytt Mag. Zool.* 10: 67—123.

The Impact of Climate on Scandinavian Populations of the Sander, *Stizostedion lucioperca* (L.)

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I. INTRODUCTION

The sander,¹ *Stizostedion lucioperca* (L.) is distributed over central and eastern Europe. The distri-

¹ The vernacular name sander is preferred to pikeperch. *Coregonus albula* is named cisco. Otherwise the scientific and vernacular names recommended by BANARESCU *et al.* (1971) are used.

bution area was mapped by HANKO (1932), DEELDER and WILLEMSSEN (1964) and BANARESCU *et al.* (1971). It seems that the species is a principal inhabitant of lakes and rivers belonging to the Black Sea and Caspian Sea drainages.

In the postglacial period the sander spread to the Baltic Sea basin. LÖNNBERG (1898) was the first to point out that all Scandinavian sander localities were in areas known to have been flooded by the freshwater *Ancylus* Lake, which filled the Baltic basin 9,000—7,500 years ago. Later authors have followed EKMAN (1922), who regarded the sander as an *Ancylus* relic, which means that the species has a poorer capacity to extend its range than most other Swedish freshwater fish, which also invaded the (northern) headwaters from the *Ancylus* Lake.

There are some sander localities on the west coast of Sweden and adjacent parts of Norway which were never covered by the *Ancylus* Lake (Fig. 1). These lakes were probably colonized during an early *Ancylus* period, when the area was brackish from the huge amounts of fresh water coming from the Baltic basin. LÖNNBERG (1898) and MÄÄR (1947) pointed out that the sander may grow and spawn in the brackish southern bays of the present Baltic Sea, as well as in the archipelago of Åland (TOIVONEN 1969) and off Stockholm.

The sander has been widely spread by man, also in Scandinavia. In Sweden this activity is recorded from 1866 (ARWIDSSON 1904) and may very well have started earlier. Introductions were first made with mature spawners, later eggs, fry or fingerlings were used. Generally, lakes to the north and northwest of the *Ancylus* limit (*cf.* Fig. 1) are not suitable habitats for the sander, while those south or southwest of the spontaneous range have got exploitable populations.



Fig. 1. Spontaneous sander localities in Scandinavia (after EKMAN 1922). The range of the Ancylus Lake is indicated (after FROMM 1953).

The management practice of adding artificially hatched fry to those, already spawning in a natural way, culminated in the 30's and early 40's. Fingerlings are still released in some lakes in order to increase the yield. Sander under legal size (38—40 cm) have been stocked recently in an experimental scale.

For the commercial freshwater fishery of Sweden the sander is very important. For the anglers, however, its significance does not compare to that of the walleye, *Stizostedion vitreum*, in North America. Since some stocks have declined and the management principles are in doubt, more research on the population dynamics is needed. The purpose of this study was to produce more evidence on the erratic reproduction, for which the species is noted. A preliminary report was published some years ago (SVÄRDSON and MOLIN 1968).

II. MATERIALS AND METHODS

Sampling

Six sander populations were studied, two of them more thoroughly, *i.e.* those of Lake Hjälmaren and Lake Mälaren. These lakes belong to the same headwater, the Norrström river, which empties in the Baltic at Stockholm. The two lakes are independent and connected by a stream, the Eskilstunaån river.

In each of the two lakes a sampling station was established in 1955. The station is a defined restricted area, where test fishing was made every year during the same season. The mesh sizes used were more varied than those of the commercial fishery. They were constant over the period, as was the number of gill nets and efforts (10, resp. 12 nights). In Lake Hjälmaren the station was a shallow bay in the western end, named Mellanfjärden. In eastern Lake Mälaren a deeper station was fished, on Lambarfjärden close to the Freshwater Research Institute. Fishing on Mellanfjärden took place during the period September 1—15, while that on Lambarfjärden occurred some time in October—November. Finally it should be pointed out, since no two individuals operate the nets with the same skill, that all the fishing was performed by one of us (MOLIN).

When we started in 1955 no statistics on the total catch of the lakes were available. In the mid 60's, however, yield data from both lakes appeared. We then realized that our fishing gave a yardstick of the population fluctuations rather different from that of the total fish statistics. This was extremely obvious at the Lambarfjärden sampling station after 1965, where our catch mounted while the general trend of the whole lake was reversed. The two nearest commercial fishermen were for various reasons not fishing as intensely as before but unfortunately we have no records of their combined catches. Our material is thus biased in spite of the efforts made. Our estimates of sander year class strength are thus uncertain for calendar years wide apart, while the dominance of one class over those nearby is well substantiated.

The scale samples from four more lakes were smaller and taken from sander caught in normal

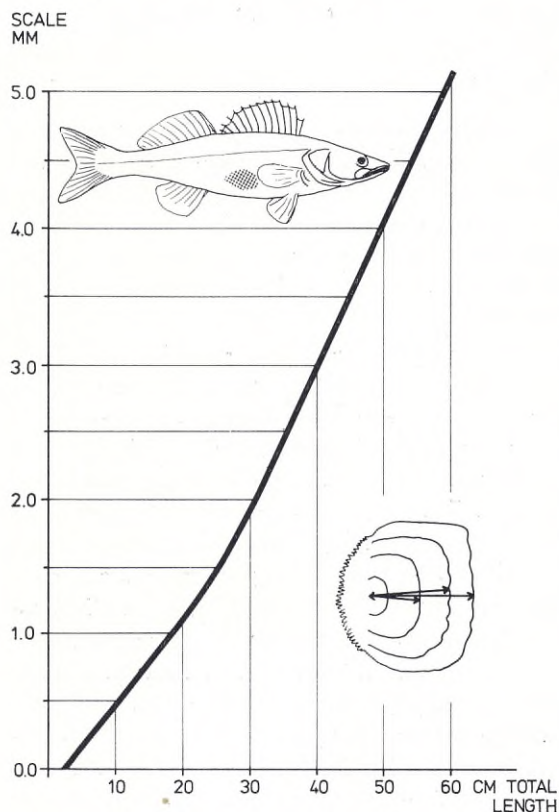


Fig. 2. Relation between the cranial radius of the scale and the total body length. Scales were taken on the marked key area.

fishing, whether of commercial or recreational type. This material could not be used to analyse year classes. It enabled growth studies, however.

Age

Scales were used for age analyses. They were all taken from a defined key area on the sander body (Fig. 2). The reading of the annuli was in some cases difficult but in a majority of fish the ageing was comparatively easy. The scales were read several times. An indirect check on the interpretation was the appearance of dominant year classes running through the annual samples.

Computation of growth

In the earlier paper no back calculation of growth was reported, since no relation curve for scale

radius on fish length was available. When some 3,000 fish were measured, such a curve was drawn (Fig. 2).

The scale radius chosen for growth computation was straightly cranial from the centre of the scale (Fig. 2). A nomograph in plastic, conforming to the curve, was fixed at the zero end. It was assumed that the allometric growth of the scale of an individual fish conformed to the curve. The coordinates of total length and total scale radius of the individual fish fixed the nomograph and the earlier growth was read from the intercepts to the annuli.

We are aware that some theoretical implications are involved in this practice. In other species, where we have been able to check with known fish lengths of younger age groups, the method was accurate enough. In view of the bias introduced by net selection, individual growth rates and Lee's phenomenon we think our accuracy is gratifying to our needs. The error by this method of course is largest for the first annulus and the back calculated length may be some ten per cent different from the true value.

III. THE LAKES AND THEIR YIELD

The highly prized muscles of the species and the capacity to stand transport and storage with smaller loss in quality than other freshwater fish, render the sander great significance to the commercial fishermen. In spite of this, statistics on the yield are rare.

For ten years, 1914—23, there was an official record of the freshwater fishery collected by the Institute of Statistics. It was realized, however, that while the cost was high, the credibility of the figures was low. No doubt this is related to the legislation of Scandinavia, where the right to fish a lake is privately owned. Mostly the right belongs collectively to the farms around the lake.

In the last few years new efforts were made to obtain figures of the yield of the commercial fishery of the four largest lakes in Sweden. In a few other lakes as well, information on the total catch has become available. Of the six lakes dealt with in this study, yield data are known from five.

The lakes represent the extremes of the sander

Table 1. Some morphological and chemical data on the six sander lakes.

	Vänern	Mälaren	Hjälmaren	Ivösjön	Vombsjön	Orsjön
River system	Göta River	Norrström—Eskilstunaån	Skräbeån	Kävlingeån	Ljusnan	
Lake area, km ²	5570	1140	484	54	12	33
Altitude, m	44	0.5	22	6	19	113
Max. depth, m	100	60	25	50	15	60
Average depth, m	25	13	6	11	7	14
Retention time, years	8	5	5	2	22 months	3 weeks
pH	6.9	7.5	7.8	7.3	8.9	7.1
Conductivity HS/20°	70	138	193	120	371	25
PO ₄ -P, ppb	5	22	26	10	42	6
Total-P, ppb	12	36	46	15	90	12
NO ₃ -N, ppb	300	570	97	50	270	5
Total-N, ppb	670	975	748	400	1.660	34
Transparency, Secchi disc.m.	4	3	2	4	1	4
Stratified	yes	yes	no	yes	no	yes

habitats in Scandinavia. Two lakes are shallow, non-stratified and eutrophic, one is huge and oligotrophic and one is a lake-resembling part of a cold, northern river (cf. Fig. 10).

Lake Vänern

Lake Vänern is the largest lake of Scandinavia. It is oligotrophic with low production (Table 1). It was regulated for hydroelectrical purposes in 1937. The water level fluctuations then became considerably smaller.

The sander of the lake probably lives in a marginal habitat. Introduced into lakes north or northwest of Vänern, the sander has mostly failed to establish. Within Vänern it spawns in bays, sheltered from the open lake by islands. Sander also spawn in the Byälven river in the northwestern part of the lake (Fig. 3). The most important spawning area is the large Dettern Bay (NORDQVIST 1906), a shallow part with clay or gravel bottoms where the Nossan river empties. The bay is considerably more fertile than the rest of the Lake Vänern (pH 7.8, conductivity 137, visibility 0.3—0.8, cf. Table 1). The second largest spawning area is the Varnums Bay, the outlet of the small River Varnan. PUKE (1952) tagged some sander in the period 1946—51 at Dettern and Varnum but found only short migrations, up to some 15—20 km away. One sander, however, was recovered 48 km from the site of tagging.

The yield of sander in Lake Vänern was some 50 or 60 metric tons during the early period 1914—23, possibly slightly more (Fig. 4). Later the yield increased and may have culminated in 1940—42 (ALMER, pers. comm.). TÖRNQVIST (1941)

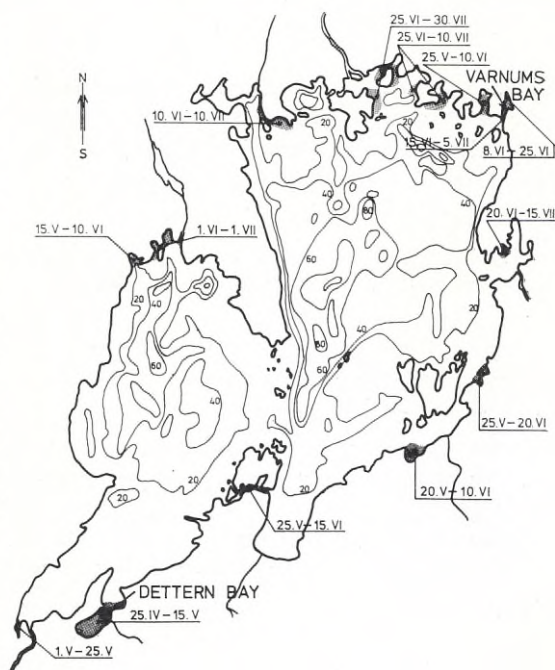


Fig. 3. Sander spawning grounds and periods in Lake Vänern.

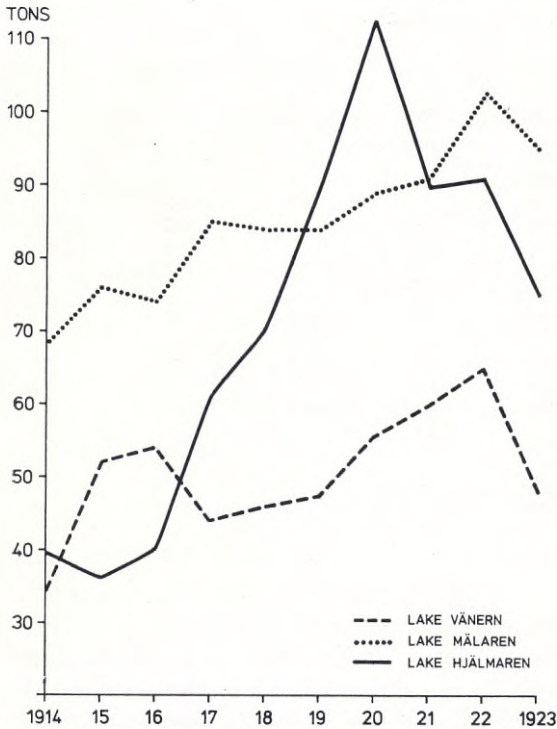


Fig. 4. Sander yields 1914—23 in the three large lakes. This decade is the only one offering official statistical records on freshwater fish.

estimated the catch in 1936 to 178 tons, which, however, may be exaggerated (ALMER). In the 1950's the yield deteriorated and the fishermen blamed the Swedish Air Force for using some

areas as target for bombing activities. Also pollution was thought to reduce the number of sander. The commercial catch was 100 tons 1962—64 but only 60 tons in 1968—71 (Table 2).

The total number of gill nets used by commercial fishermen is some 9,000. Perhaps another thousand nets are operated by recreational fishermen. Their catch is not known. ALMER estimates 90 per cent of the catch to be taken in gill nets. The rest is landed from fyke nets.

Lake Mälaren

Mälaren is the third largest lake in Sweden. It could best be described as a series of different basins, connected by shallow sounds. It is considerably more fertile than Vänern. The chemical data, given in Table 1, refers to the open parts. In some polluted bays in the north and the western end, the lake is much more eutrophic (WILLÉN 1972).

More than a hundred sander spawning grounds were mapped by RUNDBERG (1968). They are most numerous in the western end of the lake and concentrated to bays where the largest tributaries discharge into Lake Mälaren. Earlier, sander were running up four or five of the larger rivers to spawn. The very best known is the Arbogaån river, where the sander ran some 15 km up the river to the falls at Arboga. According to H. WIEDERBERG, who handled the hatchery operations there for a long time, the first spawners were

Table 2. The sander yield and largest specimen on record in six lakes (kg). The figures refer to the commercial fishery, except in Lake Ivösjön and in Lake Orsjön.

	Vänern	Mälaren	Hjälmaren	Ivösjön	Vombsjön	Orsjön
1962	112.000	—	—	1.311	6.528	—
1963	90.000	—	—	1.421	6.107	—
1964	98.000	190.000	—	1.542	6.851	—
1965	75.000	184.000	—	485	2.561	—
1966	68.000	151.000	246.000	476	4.869	—
1967	64.000	108.000	239.000	296	4.069	—
1968	62.000	136.000	202.000	356	3.563	—
1969	63.000	112.000	160.000	346	5.864	—
1970	59.000	90.000	98.000	465	7.674	—
1971	62.000	96.000	108.000	506	8.400	—
1972	—	126.000	96.000	—	3.754	—
Earlier average	1914—23	1914—23	1914—23	1956—61	introduced	1930—35
	51.000	85.000	71.000	1.814	1928—29	350
Largest sander, kg	11.0	14.3	10.5	10.6	11.1	8.2

Table 3. Commercial sander catch (kg) in the county of Västmanland, comprising the western end of Lake Mälaren and a small sector of central Lake Hjälmaren. Data from WIEDERBERG (1967).

Year	Lake Mälaren					Lake Hjälmaren		
	Galten Bay	Blacken Bay	Gran- and Västerås Bays	River Arbogaån	Total catch	Fisher men	Catch	Fisher men
1923	3.620	6.129	10.014	6.010	25.773	—	—	—
1924	7.430	9.170	12.020	5.590	34.210	—	—	—
1925	7.540	5.646	11.958	7.440	32.584	—	—	—
1926	6.810	4.810	11.120	5.300	28.039	—	—	—
1927	8.310	4.828	9.557	6.540	29.235	—	—	—
1928	9.210	5.520	10.326	6.600	31.656	—	—	—
1942	25.643	12.328	30.276	3.280	71.527	112	—	—
1943	23.936	5.135	29.655	3.242	61.968	153	5.403	14
1944	16.410	7.676	44.198	4.286	72.570	139	5.230	15
1945	10.225	3.781	18.821	2.588	35.415	70	2.685	9
1948	24.838	10.411	47.879	2.529	85.657	66	6.398	12
1953	35.216	20.460	59.350	1.454	116.480	50	7.027	10
1954	17.469	11.016	38.303	346	67.134	41	3.749	8
1955	13.248	5.539	31.282	303	50.372	40	4.313	6
1960	13.185	13.122	42.056	—	68.363	39	4.274	4
1961	10.067	14.594	35.830	—	58.491	41	2.978	6
1962	5.914	10.233	32.278	—	48.425	37	3.100	7
1963	7.332	14.951	33.934	—	56.217	35	1.820	6
1964	10.019	16.720	38.789	—	65.528	39	1.765	4
1965	6.398	11.531	42.888	—	60.817	34	2.374	5
1966	5.300	11.277	39.748	—	56.325	28	4.407	4

Total catch in Lake Mälaren correlate to the catch in Lake Hjälmaren. Coefficient of correlation 0.70 (P<0.01).

normally ripe in the river on April 25th. The spawning period occurred later in the season downstream in the Galten Bay and still later in the more western parts of Lake Mälaren, where the bulk of spawning occurred in the latter part of May and spent fish were found in early June.

There are considerable migration of sander westwards for spawning in Lake Mälaren. Sander tagged at the mouth of Arboga river were later found up to 120 km eastwards (SVÄRDSON 1948), indicating migrations over at least two thirds of the axial length of the lake.

It is generally agreed that the sander population has increased since 1914. It may be a modest increase, however, since the catch of 1922, 102 tons, was higher than that of 1970—71.

Table 3 gives some local statistics from the western end of the lake. The most interesting years around 1950 are missing but there is evidence of a peak in sander yield at this time since both 1948 and 1953 gave yields of the same order of magnitude as that of the whole lake from the 60's.

The famous River Arbogaån catch declined in the 30's and vanished completely in the 50's because of too heavy pollution. In the last few years, however, some sander have again started their run up the river, since pollution has decreased and the Ställdalen pulp mill was closed down (cf. AHL 1971).

Commercial fishermen are becoming fewer in Lake Mälaren (Table 3) as in most lakes of Sweden. Those remaining, however, increase their efforts.

Roughly 20 per cent of the recent sander catch is taken in big trap nets. These were introduced in the 30's from models used on the Baltic coast to catch herring. During the first years the trap nets produced numerous large sander. The trap nets nowadays give less yield but the nets become more numerous for every year. Some 250 are operated at present.

In the open water period about 4,000 gill nets are used to catch sander by commercial fishermen and 1,000 by recreational fishermen. During the

winter time, when fishing is more cumbersome, the proportions are 5,000 and 200 nets. Nylon nets became common in 1953.

Lake Mälaren was regulated by a dam at Stockholm harbour in 1941. The water level fluctuations, which had been severe for centuries, then became small.

Lake Hjälmarén

UGGLA (1786) mentioned the sander as the sixth species according to abundance. It was then fished mainly in the winter when several hundred gill

nets were used. Many sander were also taken in seines. The fishermen seem to have been uncertain about its spawning habits, since UGGLA says November and December were thought to be the proper time.

It is generally argued by the fishermen that the sander population became more dense when the huge crayfish population was killed by the *Aphanomyces*-disease in 1907—08. Later the sander has probably become still more numerous, except for the 60's (Table 2).

RUNDBERG (1971) surveyed the trends of the fishery in Lake Hjälmarén:

Total yield		1914—23 ¹ 213 tons	1947—50 ²	1960—65 ²	1966—69 ¹ 290 tons
Sander	per cent	30	41	52	73
Perch	„	43	28	27	14
Pike	„	13	23	13	9
Burbot	„	9	5	7	2
Whitefish (<i>Coregonus</i>)	„	5	3	1	2

¹ Catch of the entire lake.

² Catch of Örebro county (western end of the lake).

The figures conform to the idea that the sander has become progressively more abundant. Lake Hjälmarén certainly has become more eutrophic during the same period.

Table 3 shows the catch in a small northern sector of the lake. The sander catch correlates significantly to that of Lake Mälaren. Simultaneous population fluctuations and dwindling numbers of fishermen, as well as the nylon peak of 1953 contribute to this correlation.

The spawning starts in the Mellanfjärden area around May 10 and in the deeper eastern part of the lake it occurs in the beginning of June (RUNDBERG, pers. comm., ALM 1917).

Spawning grounds occur along the shore almost everywhere but there is also a general migration to the west for spawning, to the east for fattening or wintering. The most important tributary, the Svartån river, empties at Örebro, at the western end of the lake.

The sander of Lake Hjälmarén is smaller than that of Lake Mälaren. The average fish caught is below 1 kg. In the last few years experimental mid-water trawling has given some large sander, up to 8 kg. It should be noted that the sander of Lake Hjälmarén has no cisco (*Coregonus albula*)

to prey on, like those of the lakes Vänern, Mälaren, Ivösjön and Orsjön (see below). The smelt, however, occurs in Lake Hjälmarén.

Fyke nets, copied 1910 from those used in Lake Vänern, are operated and take an estimated 20 per cent of the yield. Some 3,000 gill nets are used in summer time, one third of them by recreational fishermen. In winter time the commercial fishermen dominate the fishery and operate 3,000 out of the 3,500 gill nets used.

The statistics (Table 2) refer to the commercial fishery only.

Lake Ivösjön

This lake is smaller than those discussed so far (Table 1). The sander is native to the lake, since the Ancylus Lake covered the northeastern part of the province of Skåne (Scania).

Lake Ivösjön is about as fertile as Lake Mälaren. Most of its area is filled by a large island. It is deeper than Hjälmarén and stratified. Recently some oxygen deficiency has occurred annually. The lake was described by ALMER (1971).

The sander was fairly numerous in the 40's and early 50's. In 1956—61 the average yield was 1.8 tons but in recent years the catch is very low

indeed (Table 2). There has been intense local discussion about the causes of the decline. The sudden drop of the catch in 1965 correlates to the outbreak of a diphyllbothrian infection in four other fish species which discouraged most recreational fishermen for some years. Nowadays, this shock is overcome, but the catch is still low.

Most spawning takes place in May in two bays of the northeastern part of the lake. Some sander spawn at a considerable depth, about 8 m, in a restricted area about 25th of June.

Only two commercial fishermen fish the lake. Besides, recreational fishermen number almost 1,500. Dominating gears are hooks, fyke nets and gill nets. Some 700 gill nets are used as estimated by ALMER. In the 50's considerable sander fishing was performed by trolling.

The Nymölla pulp mill was established on the outlet in the 60's. From 1963 the water level of Lake Ivösjön is controlled.

It should be mentioned that Lake Ivösjön is one of the very rare cases in Sweden where a crayfish population is recently becoming more dense (SVÄRDSON 1972). If the correlation in time between sander increase and crayfish disease in Lake Hjälmarén be causal, the reverse *might* be happening in Lake Ivösjön.

Lake Vombsjön

This lake is shallow, highly productive and not stratified. Lake Vombsjön is a smaller copy of Lake Hjälmarén (Table 1).

Lake Vombsjön was never covered by the Ancylus Lake and consequently had no native sander. The species was introduced in 1928, when 50,000 eggs were planted. Next year some 8,000 fingerlings and 125 adult fish were added. A population built up rapidly and has become still more dense in later years due to proper management. Young sander are found in the outlet in some years. They are thin and indicate a population spillover.

Two commercial fishermen dominate the fishery. They use some big trap nets, taking large number of coarse fish as well. Immature sander have been put back into the lake, specimens of 7—8 kg are taken annually.

Spawning grounds, at a depth of 2—3 m, lie in the central part of the lake. Sander may start to aggregate there in the last days of April in warm spells but some may also be found there until the first week of June.

The annual catch varies between 2.5 and 8.5 tons, depending on whether the big traps have operated efficiently or not (Table 2). This in turn depends on the water level, which was recently controlled to serve other demands. Low water is detrimental for the traps which are erected on firm fundaments.

Smelt was introduced with the sander. If they ever became established, they are long since eradicated. Cisco occurred — as introduced — in the 40's but are now gone as well. The sander of Lake Vombsjön thus is compelled to have a diet different from that of the populations in the other lakes studied.

Lake Orsjön

This lake differs strikingly from the others (Table 1). It is essentially a wide section of the Ljusnån river, which gives the lake a very short retention time, irregular stratification with density currents and a rather severe temperature regime. The lake is oligotrophic, the conductivity being less than half of that of Lake Vänern.

Sander spawning takes place in the northern part of the lake, on clay and stone bottoms around June 25.

The sander is native to the lake, which is also inhabited by smelt and cisco. The sander population is sparse and noted for its irregular fluctuations. The yield records are few and uncertain. In the 30's some 350 kg was estimated as an average annual yield. In connection with recent hydro-electrical changes of the river flow, the yield was again estimated in the 60's, from the farmers' statements. This time the yield was said to be much higher, some 2,300 kg. We think, however, these latter figures are highly biased by the fact that some recompensation might be included in the verdict from the water court. We have therefore preferred the figure from the 30's which is also more in agreement with the yield trend given by the other lakes studied.

IV. DOMINANT YEAR CLASSES

General trends

ALM (1917) noted that the fishermen of Lake Hjälmaren were aware of the appearance of a new "hatch" of sander by the number of small specimens entangled by their teeth in the gill nets. The year class 1914 was probably rich according to ALM. It can be seen from the catch statistics 1914—23 in the three big sander lakes of Sweden (Fig. 4) that the records support the idea that 1914 had produced a rich year class of sander in all the lakes.

TIDEMAN (1933) studied the sander populations of four lakes in the province of Östergötland. Lake Roxen is a well-known sander lake and the species also occurs in the smaller lakes Glan, Ämmern and Svinstadsjön. All lakes gave poor sander yields 1925—29. Fingerlings were released in Lake Roxen in 1929 but no management was started in the other lakes. In 1930, however, young sander appeared in great numbers in all four lakes. The sander were not aged by TIDEMAN but were very probably born in 1927, which corresponds to the weight reported. In 1927 a very dominant sander year class was born in the eastern brackish Finnish Bay, as detected by SEGERSTRÅLE (1936) on scale samples.

TESCH (1962) found that the year class 1948 of sander was dominant in Lake Müggelsee near Berlin as well as in the brackish Stettiner Haff of the Baltic.

Year class 1953 was again dominant in Lake Müggelsee (TESCH 1962) and, to judge from age group III caught in spring, also in the huge Lake Ladoga (RITZVANOV 1970). We found (SVÄRDSON and MOLIN 1968) the 1953 class to be dominant in Lake Hjälmaren as well as in Lake Mälaren.

We also found 1959 producing dominant year classes in both lakes. Again, in Lake Ladoga the sparse sander population also produced a dominant class (RITZVANOV 1970) and, more surprisingly, a number of lakes in North America reacted similarly. Two lakes in New York, Oneida Lake (FORNEY 1966) and Black Lake (LETENDRE and SCHNEIDER 1969), two lakes in Wisconsin, Pike Lake (MRAZ 1968) and Lake Winnebago (PRIEGEL 1970) and finally Lake Erie (PARSONS 1971) and Lake Ontario (CHRISTIE 1973)

also produced dominant walleye year classes in 1959.

There is a tendency for other species of fish to have dominant year classes in the very same years. SEGERSTRÅLE found 1927 to be a good year also for other species. 1953 is a year of dominant classes of several Swedish freshwater fish (*Coregonus*, *Thymallus*). 1959 produced a dominant class of pumpkinseed sunfish in Oneida Lake (FORNEY 1966) and of troutperch in Lake Winnebago (PRIEGEL 1970). This tendency is favourable for the sander, which is a predator already at a size of 4—5 cm.

The evidence, of course, must be interpreted thus that climate influences the production of dominant sander year classes. ÄNGSTRÖM (1946) records the summer of 1914 to be extremely hot, especially July, in the long series of climate registrations at Stockholm.

1927 was again very hot (ÄNGSTRÖM 1946) and SEGERSTRÅLE (1947) found that it was the hottest early summer in at least 35 years in southern Finland. He found that the bream grew extremely fast this summer, as evidenced by the scale readings.

Temperatures were above normal in May, June and August in 1953 in large parts of central and northern Europe. In 1959 the whole period May—August was warmer than average in places like Duluth, Toronto, Berlin and Stockholm.

15 year classes of lakes Hjälmaren and Mälaren

In order to get a score of the strength of the year classes we added all sander caught during their third, fourth, fifth and sixth growth period. (Tables 4 and 5). It was found that the classes could differ in their stepwise cumulative score. The class 1959 of Lake Hjälmaren was rather moderate as judged by the catch in 1963 and 1964. The exceptional score of year class 1966 in Lake Mälaren on the other hand was dominated by the catches in 1968 and 1969 while that of 1970 and 1971 was moderate. It is not known which factors were responsible for this variation.

The larger material confirmed the result already presented on the first eight year classes (SVÄRDSON and MOLIN 1968). There is a pronounced parallel trend in the year class dimensions of the two independent lakes (Fig. 5).

Table 4. Sander catch in Lake Hjälmaren (numbers), adjusted to a constant effort of ten nights a year.

Year of catch	I+	II+	III+	IV+	V+	VI+	VII+	VIII+	IX+	X+	XI+	Total
1955	—	34.0	1.0	—	—	—	—	—	—	—	—	35.0
1956	—	9.1	111.7	0.9	—	—	—	—	—	—	—	121.7
1957	—	12.0	9.0	51.0	2.0	—	—	1.0	—	—	—	75.0
1958	—	5.0	28.0	12.0	18.0	—	—	—	—	—	—	63.0
1959	2.2	44.4	14.4	11.1	1.1	1.1	—	—	—	—	—	74.3
1960	—	24.0	18.0	—	—	—	1.0	—	1.0	—	—	44.0
1961	—	29.0	9.0	—	—	—	—	—	—	—	—	38.0
1962	—	2.0	39.0	2.0	1.0	—	—	—	—	—	—	44.0
1963	1.0	7.0	17.0	73.0	2.0	—	—	—	1.0	—	—	101.0
1964	2.0	9.0	14.0	23.0	63.0	—	—	—	—	—	—	111.0
1965	—	1.0	8.0	21.0	26.0	12.0	—	1.0	—	—	—	69.0
1966	1.0	3.0	26.0	17.0	36.0	29.0	8.0	—	—	—	—	120.0
1967	1.0	2.0	2.0	19.0	12.0	9.0	6.0	—	—	—	—	51.0
1968	7.0	84.0	5.0	8.0	13.0	6.0	7.0	2.0	—	—	—	132.0
1969	7.0	85.0	26.0	3.0	—	2.0	—	—	—	—	—	123.0
1970	3.0	51.0	34.0	5.0	—	—	1.0	—	—	—	1.0	95.0
1971	—	32.0	54.0	6.0	—	—	—	—	—	—	—	92.0
1972	2.0	5.0	60.0	19.0	2.0	—	—	—	—	—	—	88.0
Total	26.2	438.5	476.1	271.0	176.1	59.1	23.0	4.0	2.0	—	1.0	1,447.0
%	1.8	29.7	32.2	18.3	11.9	4.0	1.6	0.3	0.1	—	0.1	100.0

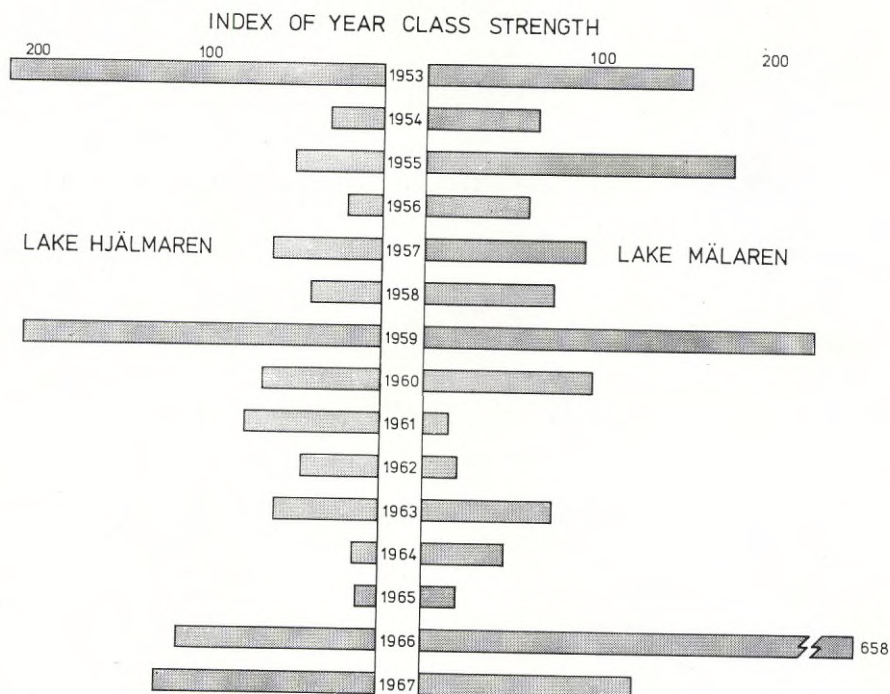


Fig. 5. The scores of fifteen year classes in two lakes.

Table 6. Correlation coefficients for strength of sander year classes and summer temperature. Airtemperature was recorded as deviation from average at Stockholm and Örebro. A=fifteen year classes 1953—67. B=the same, but 1966 omitted. The significant coefficients are marked out.

Month	Lake Mälaren				Lake Hjälmaren	
	A Corr.coeff.	P.	B Corr.coeff.	P.	A Corr.coeff.	P.
April	0.39	> 0.05	—	—	0.43	> 0.05
May	0.03	> 0.05	—	—	0.09	> 0.05
June	0.49	> 0.05	0.29	< 0.05	<u>0.62</u>	> 0.01
July	0.49	> 0.05	<u>0.92</u>	< 0.001	0.48	> 0.05
August	0.21	> 0.05	<u>0.92</u>	< 0.001	0.48	> 0.05
April—May	0.25	> 0.05	—	—	0.36	> 0.05
May—June	0.30	> 0.05	—	—	0.41	> 0.05
June—July	<u>0.60</u>	> 0.01	<u>0.82</u>	< 0.001	<u>0.75</u>	< 0.01
July—August	0.35	> 0.05	—	—	0.48	> 0.05
June, July, August	0.47	> 0.05	<u>0.92</u>	< 0.001	<u>0.69</u>	< 0.01

Table 6 shows the correlation coefficients for year class strength and deviation from average air temperature. The air temperature is from the official records at Stockholm (close to the Lambarfjärden station in Lake Mälaren) and at Örebro (near Mellanfjärden of Lake Hjälmaren). The highest correlation coefficients, 0.60 and 0.75 appear for the June—July temperature. In Lake Hjälmaren also the combined period June—August gives a significant correlation.

The year class 1966 of Lake Mälaren is outstanding. At least in part this is due to the biased sampling at our station in the late 60's when commercial fishermen in the neighbourhood were not as busy as before. This extreme year class accounts for a lot of the total variation. If the class of 1966 is excluded, the correlation coefficient between year class strength and the air temperature of July and August rises to 0.92 which is, of course, very significant.

The new analysis stresses the importance of the real summer months, while the impact of May becomes negligible and even June is not as important as we thought in our preliminary report.

Climate and yield trends

The regression of year class strength on air temperature for June—July in Lake Hjälmaren was

$$Y = 74.0 + 24.2 X$$

It was assumed that this equation would also describe the relation between year class score and

air temperature in Lake Vänern and Lake Ivösjön (which is, of course, not probable except as a rough estimate). From the official records of air temperature at Vänersborg (close to the Dettern Bay of Lake Vänern) and Kristianstad (close to Ivösjön) a number of year class scores were calculated.

It was further assumed that only sander in their sixth to ninth summer were fully vulnerable to the fishery. The sum of the score for four consecutive year classes, e.g. 1950—53 was regarded as the potential catchable population of the calendar year 1958. The year classes 1951—54 made up the potential catch of 1959 etc. No effort was made to convert numbers of sander into weight. Fig. 6 shows the result obtained when this potential catch is compared to the real catch.

For a period of 30 years there is a general parallel trend of a declining potential population and the sander yield in Lake Ivösjön.

In Lake Vänern two different series of commercial sander landings illustrate the trend. One is the records of the SALS Fishselling Association, working on southern Vänern. The other is the Kristinehamn's Cooperative Fish Sales Union, landing fish from the northeastern part of the lake. The curves indicate that part of the substantial decline of the Vänern sander catch might be attributed to a change of the summer temperature climate.

The evidence from the parallel dominant year

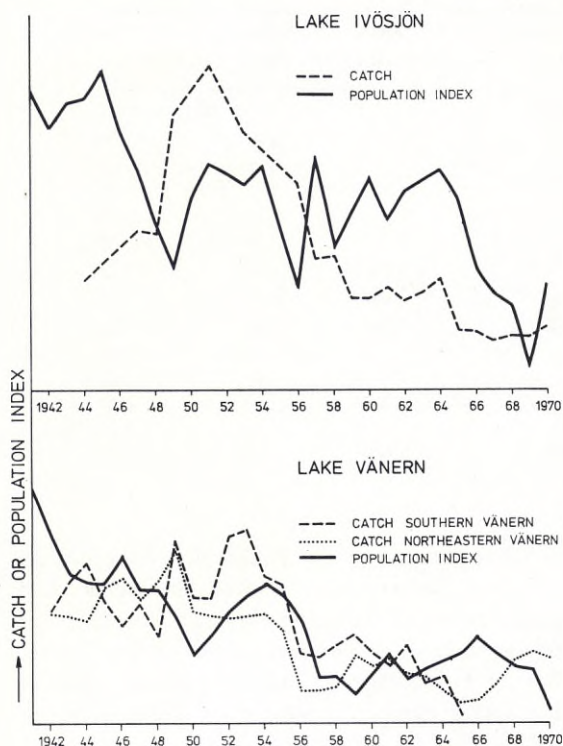


Fig. 6. Real catch of sander compared to potential population available, as calculated from air temperature records.

classes in widely separated lakes indicates a climatic factor being responsible. The long term trends seem to relate to climate in a similar manner, indicating that the total mortality from eggs to catchable sander is related to the general water temperature during the first summer of life.

Temperature and water level during the spawning period

The sander is a warm-water species compared to its American relative, the walleye. The preferred temperature for spawning is not lower than 11–13°C for the sander (DEELDER and WILLEMSEN 1964, TESCH 1959, NORDQVIST 1905, RITZVANOV 1970) but 4.5–10°C for the walleye (ESCHMEYER 1948, RAWSON 1957). The sander may migrate for spawning upstream a short distance (15–20 km) while the walleye may move about 100 miles (160 km) (ESCHMEYER (1948), PRIEGEL (1970)). Both spawn on the same type of

bottom while the sander prefers more turbid water than the walleye.

WILLEMSEN (DEELDER and WILLEMSEN 1964), WIDERBERG (1941) and MUNTYAN (1966) reported that hatching does not occur below 9°C, is most rapid at 25°C (2–3 days), gives the highest percentage fry at 12–14° and the largest fry at 11.5°C. WIDERBERG (pers. comm.) and BELYY (1968) stress the vulnerability of the sander fry during the first 3–4 days when they migrate vertically up and down but do not swim horizontally. During this period high turbidity of the environment, or currents, may reduce the mortality from predators. It seems that the sander is more adapted to the turbidity, while the walleye mostly uses the currents.

Many authors have stressed the risk that the tiny fry be starved by inadequate amount of plankton food (*cf.* TESCH 1962) or be taken by predators. KLEINERT and DEGURSE (1968) found, however, that walleye fry could starve two weeks in normal temperature before starting to die and the sander may thus have a smaller risk of dying from starvation in nature than often thought.

In the Dettern Bay, where the temperature may drop considerably from day to day, due to the shallow water and the high winds from the more open parts of Lake Vänern, the fishermen say that, during the period of sander hatchery work, all sander eggs could whiten and die in cold spells. Records from 1972–73, however, do not indicate that temperatures below 9°C often occur, (Fig. 7). 1972 was by the fishermen thought to be a “bad sander spring”.

For the years when sander year classes are known in Lake Mälaren, the spring temperature (average for five-day-periods) at Stockholm is given (Fig. 8). It appears that the May temperature is quite low. There is no obvious relation to year class strength.

The water level, however, may influence year class strength. The two best year classes were born in years having also the highest water level in spring. In 1959 the water level was high in mid-April while in 1966 the water level was very high in mid-May, because of the late spring.

1966 was outstanding among the fifteen year classes in Lake Mälaren. Its enormous score may, however, be biased by the fact that the efforts of

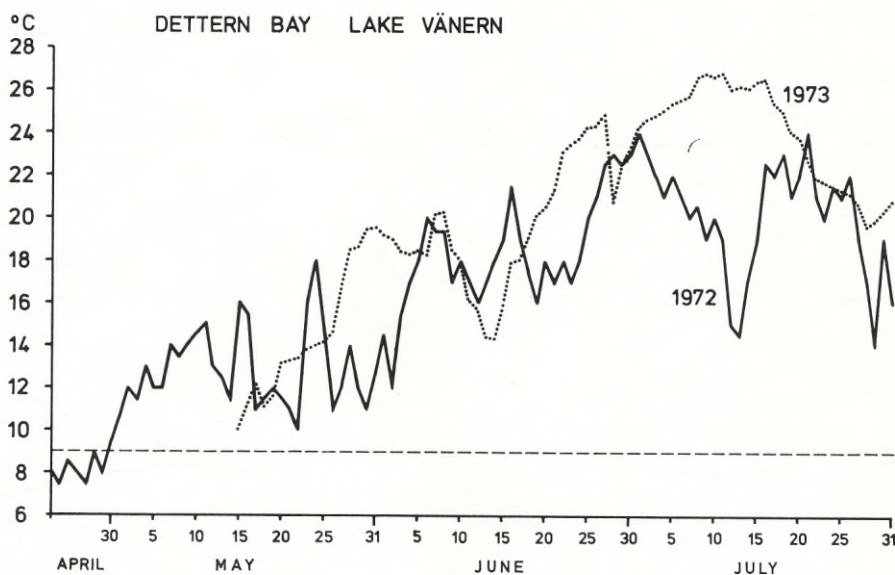


Fig. 7. Surface water temperature of two sander spawning periods in Dettern Bay.

the commercial fishery going on not far from our station had decreased. Though no doubt a very dominant class, its absolute score was probably exaggerated. When this class was omitted from the series, the correlation to summer temperature became much higher (Table 5).

The high water in May 1966 produced a very dominant year class also of pike in Lake Mälaren. Impoundments during the first year tend to produce good growth and excellent survival in fish. ELROD and HASSLER (1969) found walleye and pike to have rich year classes the year when Lake Sharpe, South Dakota was created by a dam. It is reasonable to assume that the nutrients, and the increased turbidity of rising waters in May, may have favoured the survival of sander fry. For 1959 this factor may have been additional only, in view of the widespread parallel trend of dominant sander or walleye classes in that year.

It should be mentioned that the Dettern bay of Lake Vänern was very turbid in years of high water, before Vänern was controlled in 1937. The historic peak of sander yield in Lake Vänern occurred about 1941 and was thus based on year classes born before the lake level was controlled by a dam at Trollhättan.

Summing up, there is some evidence that ex-

ceptional high water during the spawning period of the sander may have some influence on the subsequent dimension of the year class. Since water levels tend to fluctuate less parallel over wide areas than the temperatures, the effect of this second factor may be subsidiary in lakes with a sizeable sander population. In lakes where sander just "hang on" in low numbers for considerable periods, but suddenly explode in a strong single year class, the rôle of the water level may be more prominent.

V. GROWTH

Sex ratio and sex differencies in growth

Sex ratio of the sander and the walleye is often distorted in catches taken during the spawning period. Male sander guard the nest for some time while the male walleye tend to remain on the spawning grounds after the females have left (PRIEGEL 1970).

Our sander were taken in late summer or autumn. The sex ratio was even.

	Males	Females	Total	Per cent males
Lake Hjälmaren	710	772	1,482	47.9
Lake Mälaren	1,135	1,113	2,248	50.5
Total	1,845	1,885	3,730	49.5

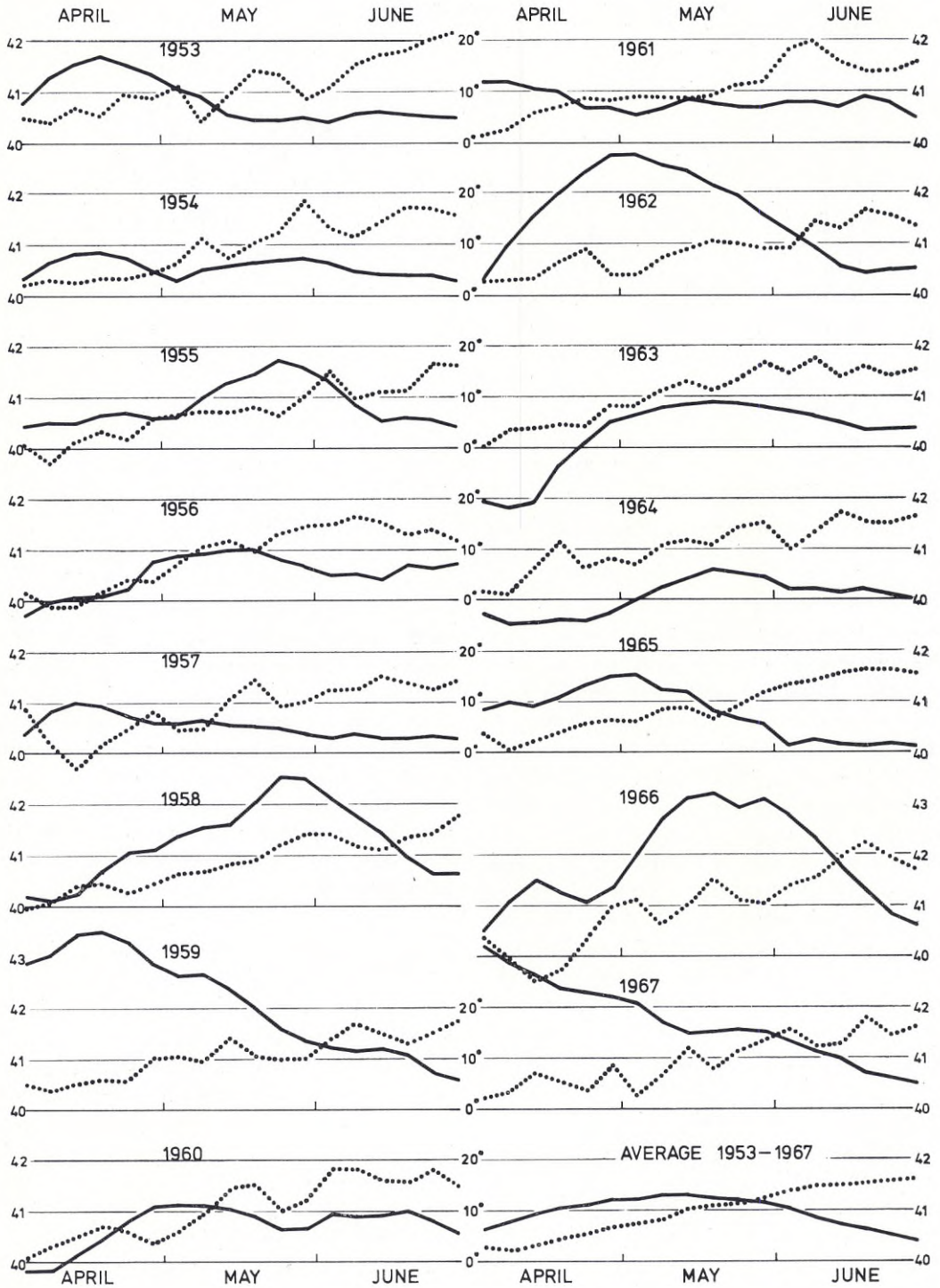


Fig. 8. Air temperature (broken line) and water level records at Stockholm for the 15 years, from which the sander year classes are scored.

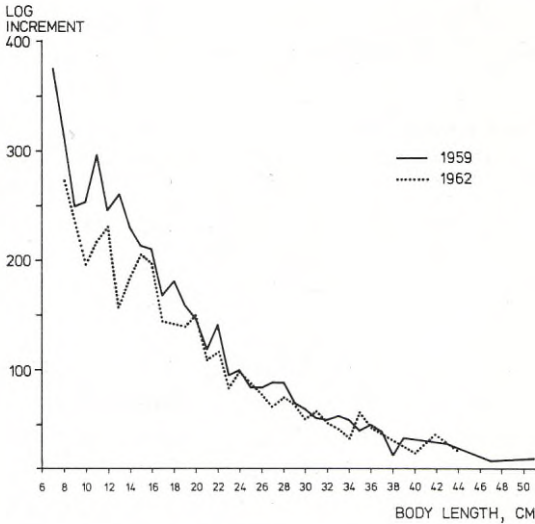


Fig. 9. Growth increments of all sander sampled living in Lake Mälaren during a warm and a cold summer, arranged according to fish size.

OLSON (1968) discussed the sex ratio of the walleye. Most samples in lakes were rather balanced while pond-reared fingerlings varied widely, indicating that environmental stress influenced the survival and favoured the males.

The back-calculated growth was similar during the first five years of the Mälaren sander.

Age group	Males	Females
I	109 mm (1,135 sp.)	109 mm (1,113 sp.)
II	198 (1,120)	196 (1,108)
III	286 (760)	286 (721)
IV	340 (383)	344 (382)
V	384 (166)	385 (167)
VI	437 (45)	452 (40)
VII	515 (13)	527 (9)
VIII	583 (7)	588 (2)

The differential growth, if real, is very slight and the females tend to grow better at higher age. This correlates to their later maturity (SVÄRDSON and MOLIN 1968). RITZVANOV (1970) found sander males in Lake Ladoga to grow more slowly than the females from the fifth year, but he suggests they grow better than the females in early life. This is probably wrong and correlated to their earlier maturity which had biased the samples favouring fast growing individuals. The walleye females grow better than the males from the

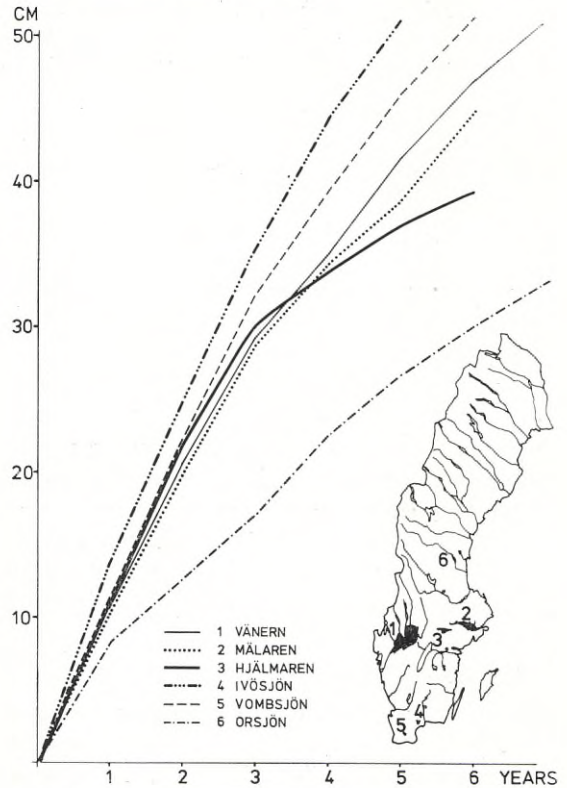


Fig. 10. Growth curves of sander from six lakes. Further details are included in Table 7.

third year (ESCHMEYER 1948, HILE 1954, MRAZ 1968) or, in colder climate, not until the seventh year (RAWSON 1957). The two species seem to be rather similar in this respect but possibly the sander has a less pronounced growth difference between the sexes than the walleye.

Summer temperature

In reading the sander scales it was often rather striking that growth was better in some years known to have been warm. To illustrate this, the method of LARKIN *et al.* (1956) was adopted. The growth increment (Fig. 9) was plotted for all sizes of sander living in Lake Mälaren during 1962 (cold) and 1959 (warm). The method could not be used for 0+ fish but according to the graph the better growth during the warm year should be even more pronounced in fingerlings than in older fish. ZAWISZA and BACKIEL (1972) found the

Table 7. Growth of sander in different lakes.

Lake	Number of fish	Back-calculated total length in mm, at end of year									
		1	2	3	4	5	6	7	8	9	10
Vänern	451	112	207	292	350	416	470	510	554	600	636
Mälaren	2,248	109	197	286	342	385	446	520	584	616	650
Hjälmaren	1,482	110	218	303	339	369	394	460	543	603	—
Ivösjön	50	138	248	352	442	511	570	635	677	732	763
Vombsjön	50	108	221	321	392	459	512	554	602	640	660
Orsjön	52	83	126	170	225	267	300	331	364	411	450
Glan	19	108	201	303	380	455	544	575			

growth of the sander be accelerated 3—4 times in an artificially heated lake. There can be little doubt that one major factor contributing to the strength of year classes is the faster growth during warm summers.

SMITH and PYCHA (1961) noted better growth rate of the walleye in Red Lakes, Minnesota during the warmer 30's than in the cooler 50's.

Growth rates in six lakes.

The sander growth rate of the two most southern lakes was fast, while that of the northernmost lake was very slow (Fig. 10, Table 7). The three

sander populations of the large lakes of middle Sweden have rather similar growth, in spite of the fact that Lake Vänern is oligotrophic while Lake Hjälmarren is eutrophic.

The excellent growth rate of the sander in Lake Ivösjön correlates to a sparse population, abundant smelt and cisco and a favourable climate. The Vombsjön sander have a favourable climate but miss the preferred prey (smelt and cisco) and feeds predominantly on perch and roach. The Orsjön sander has abundant prey food but a very unfavorable climate which must be responsible for the poor growth.

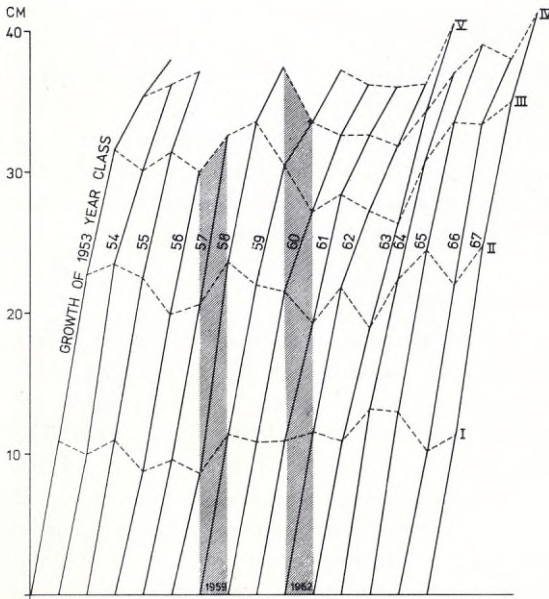


Fig. 11. Growth of individual year classes in Lake Hjälmarren.

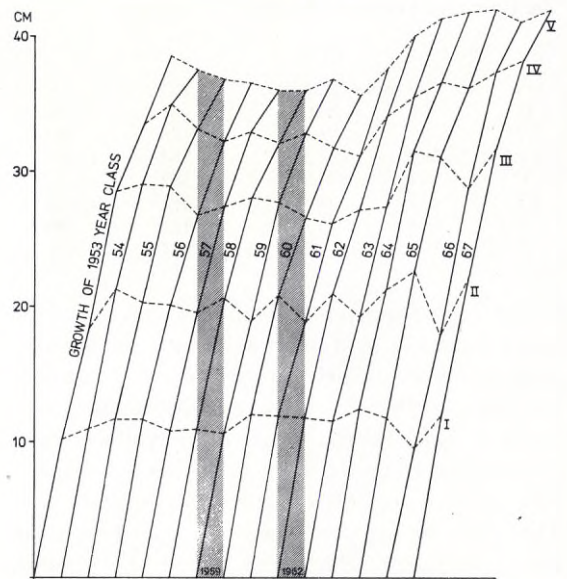


Fig. 12. Growth of individual year classes in Lake Mälaren.

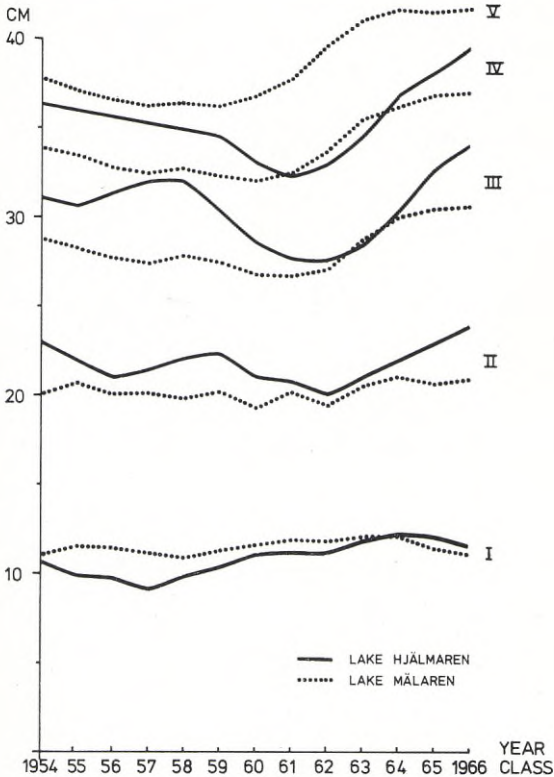


Fig. 13. Smoothed curves showing the changes in year class growth rates.

None of the populations, however, compare with the first generations of sander in Lake Ymsen (VALLIN 1929) or those of Riga Bay in the Baltic (MÄÄR 1947).

Growth of different year classes

Sander belonging to the fifteen year classes have been treated separately in Lake Hjälmaren and Lake Mälaren (Fig. 11 and Fig. 12). It appears that a warm year (1959) tends to "raise" the growth curves while a cold year (1962) tend to press them down. But clearly there are some long term tendencies involved also.

In Fig. 13 these trends have been augmented by a running three years' average for each age group. There is a most remarkable parallel trend of both lakes in time, showing a progressively improved growth rate during the last part of the period

studied. The sander of Lake Hjälmaren, however, has a more pronounced fluctuation of growth.

The yield of the sander has declined drastically in both lakes during the late 60's (Table 2). The intensity of the fishery is so high that the yield no doubt depicts the population trends. The conclusion must be that the population decline has produced an improved growth rate.

As mentioned in the earlier report (SVÄRDSON and MOLIN 1968) the weight of the sander in Lake Hjälmaren during 1961—65 was, within corresponding length groups, lower than in 1955—60. Not only were the fish thin and in poor condition, but eggs from unidentified parasites were found in their intestines as well. The fishermen reported that *smelt were almost gone* and thought the sander were thin because of scarcity of this preferred food. This was probably correct, as there is no cisco in Lake Hjälmaren which may serve as an alternative principal prey for the sander.

What the fishermen did not recognize was, that the scarcity of smelt most probably was caused by overexploiting by the sander of its food resource. The more pronounced growth fluctuations of the sander of Lake Hjälmaren thus correspond perfectly to what is known about the greater abundance of this stock and more narrow prey food basis.

Considering the fluctuations in growth rate within Lake Hjälmaren during the period studied, the sander growth in the early 20's (FREIDENFELT 1922) is within the recent limits (Fig. 13).

The growth analysis has shown that sander, especially the younger ones, grow faster in warm summers. The more dense year classes, produced in such summers, display a delayed interference with growth especially in the older age groups and in very good sander habitats where the species may reach — and supersede — the limit of abundant forage fish supply.

VI. SANDER PREDATION EFFECTS

Introduction into new environment

The sander is an unspecialized predator known to feed preferably on smelt but having a wide range of prey species. It takes relatively small prey and is a clumsy hunter, often swallowing the prey tail

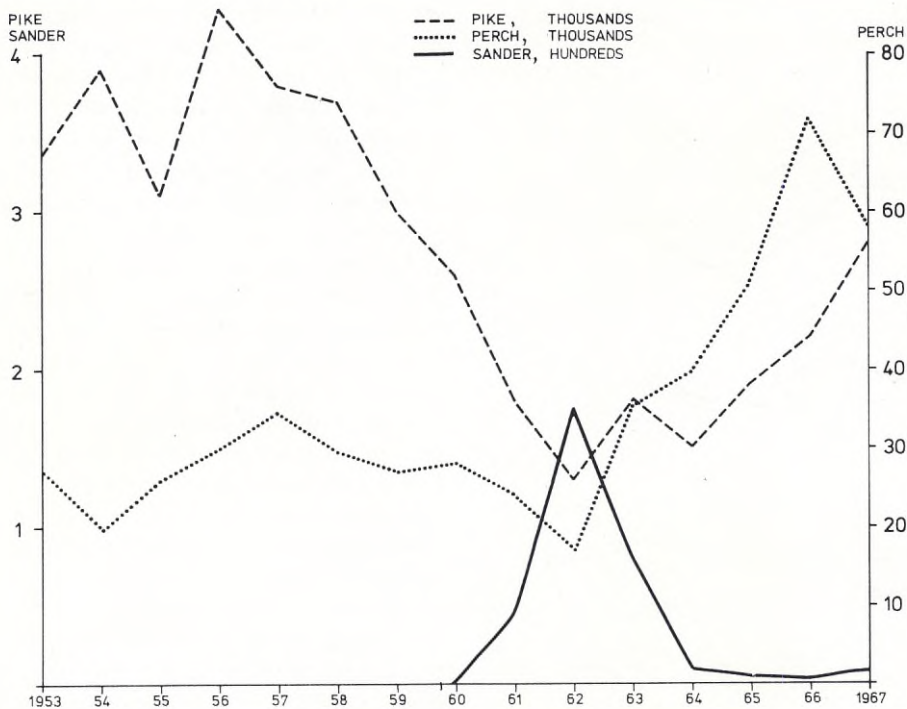


Fig. 14. Catch records from Lake Erken where sander were introduced 1958.

first. It is nocturnal or hunts at dusk and dawn. The eyes are specialized for reduced light conditions which may be a further adaptation to turbid waters.

The impact of sander on its prey species is most easily studied when sander are introduced into new lakes. VALLIN (1929) described the consequences of the introduction of sander into Lake Ymsen (14.5 km²) in 1911. The first catch of sander was in 1914 and the yield rapidly rose to a staggering 13 tons in 1918, *i.e.* almost a ton per km². Later the yield declined to about 4 tons. The first generations of Ymsen-sander were above 50 cm total length in their fifth summer, which means a record growth rate (*cf.* Table 7).

The population explosion of the new predator in Lake Ymsen heavily reduced the prey populations, especially that of perch. During the period 1918—27 the annual catch of perch dropped from 1,175 kg to 87, that of bream from 2,435 to 69 and of roach from 285 to 5. The general human food shortage in the last war and first postwar years naturally increased the fishing effort. Later,

however, the impetus to fish grew smaller, which strengthened the decline in yield. The pike was first reduced from 2 tons (1918—19) to 0.8 tons (1925—26) but suddenly recovered in 1927.

Sander were introduced 1913—15 into Lake Ellestadsjön in the province of Skåne. They spread downstream to Lake Snogeholmsjön, where a sibling population built up. In both lakes the yield of bream was heavily reduced to about ten per cent of the former level. Perch were reduced to a third or a quarter of the pre-sander density. NORDQVIST (1931) referred the change in the perch to the impact of sander. The bream had been heavily fished during the period and the interpretation of that decline was therefore ambiguous.

DAHL (1962) noted in the Danish Lake Arresø that, 15—20 years after the sander introduction, the pike catch had declined to less than a third and the perch had almost disappeared. However, during the time lapse between yield data in Lake Arresø, the eutrophication had progressed and turbidity increased, which may have contributed to the change.

When a new lake is created by a dam in a river, pike and sander tend to change in reversed directions (NIKOLSKI 1957) and the same tendency was reported by ELROD and HASSLER (1969) for northern pike and walleye in South Dakota.

A most interesting case was the sander introduction into Lake Erken (25 km²) in 1958 (Fig. 14). Ten thousand fingerlings were released in late summer and the yield culminated in 1962. The reproduction of the new species was very poor, as is sometimes the case. That made the effects of sander predation even more clear.

The Erken pike population declined as the new sander grew and probably preyed on the smaller pike. The pike yield fell from 3—4,000 specimens annually, to only about 1,500. Sander no doubt also preyed on the most common fish, the perch, as did also the pike. New predatory pressure from sander and lighter pressure from pike made the perch population smaller and the average catch per gill net went down from 1.2 kg in 1955 to 0.15 in 1962 (AGNEDAL 1969).

When most of the sander were gone, either by being fished out or from natural mortality, the predatory pressure on the perch was much reduced, as the (larger) pike were few. The perch population increased and the average catch per gill net rose to 0.7 kg in 1966. The yield was much higher than before, which may have been influenced by a new gear being very popular among the recreational fishermen of the lake (AGNEDAL, *op.cit.*). The effect on perch when pike is reduced was also described by Lawler (1965) from the Heming Lake experiment, Manitoba. Lawler points out that the larger pike is the more effective predator on the (yellow) perch.

It seems from this experience of introductions that the sander may have a strong influence not only on perch, bream and roach, which are normal prey species, but also on the pike.

Balanced conditions

Naturally it is much more difficult to establish the predatory effect of the sander in the multi-species community of a lake where sander is native. Predation, like competition, can best be studied in unbalanced conditions connected with new species combinations, population crashes etc. If several

species, including the sander, are all producing dominant year classes when under the same environmental conditions (temperature, water level etc.) there is a fundamental tendency for parallel fluctuations. If different age groups of the various species are exploited, the yield curves may be displaced.

ALM (1936) discussed the yields of individual commercial fishermen, who kept close records. There were several series of inversed relations between sander and perch. ALM discussed the probability of predation and was reluctant to believe it was true. TESCH (1955, 1965) surveying the perch literature was more in favour of the alternative interpretation of ALM's material to prove predation by the sander.

Two further cases are given in Fig. 15, both from Lake Hjälmaren. Hemfjärden is the westernmost bay of the lake, while Mellanfjärden is close to the place where the material included in this study was collected. In the Mellanfjärden fishing area there is an obvious inverse relation in yield between sander and perch, while this tendency is weak or non-existing in Hemfjärden. The pike population tends to fluctuate more irregularly in relation to the sander.

It is reasonable to suggest that an inverse correlation of sander/perch develops where the sander population is dense (Mellanfjärden) while the relation is irregular or positive where the species occurred in small numbers, and both fluctuate according to climatic factors (Hemfjärden is unfavourable for both species).

The same may be true regarding the different tendencies of sander/perch in the two lakes, Hjälmaren as a whole and the huge Lake Vänern. In Lake Hjälmaren the sander has increased since 1914 (*cf.* page 118) while the perch has decreased. The inverse relation in the whole lake corresponds to a very high density of the sander. In Lake Vänern, on the other hand, the sander is sparse and became more so in the last decades. It has been argued (p. 124) that this trend is caused by climatic factors. The fishermen of the lake are much concerned, not only about the sander decline but also of the simultaneous decrease of the perch. When both species react in a similar way to summer climate (*cf.* LECREN 1958) and are too sparse to influence each other in abundance, both

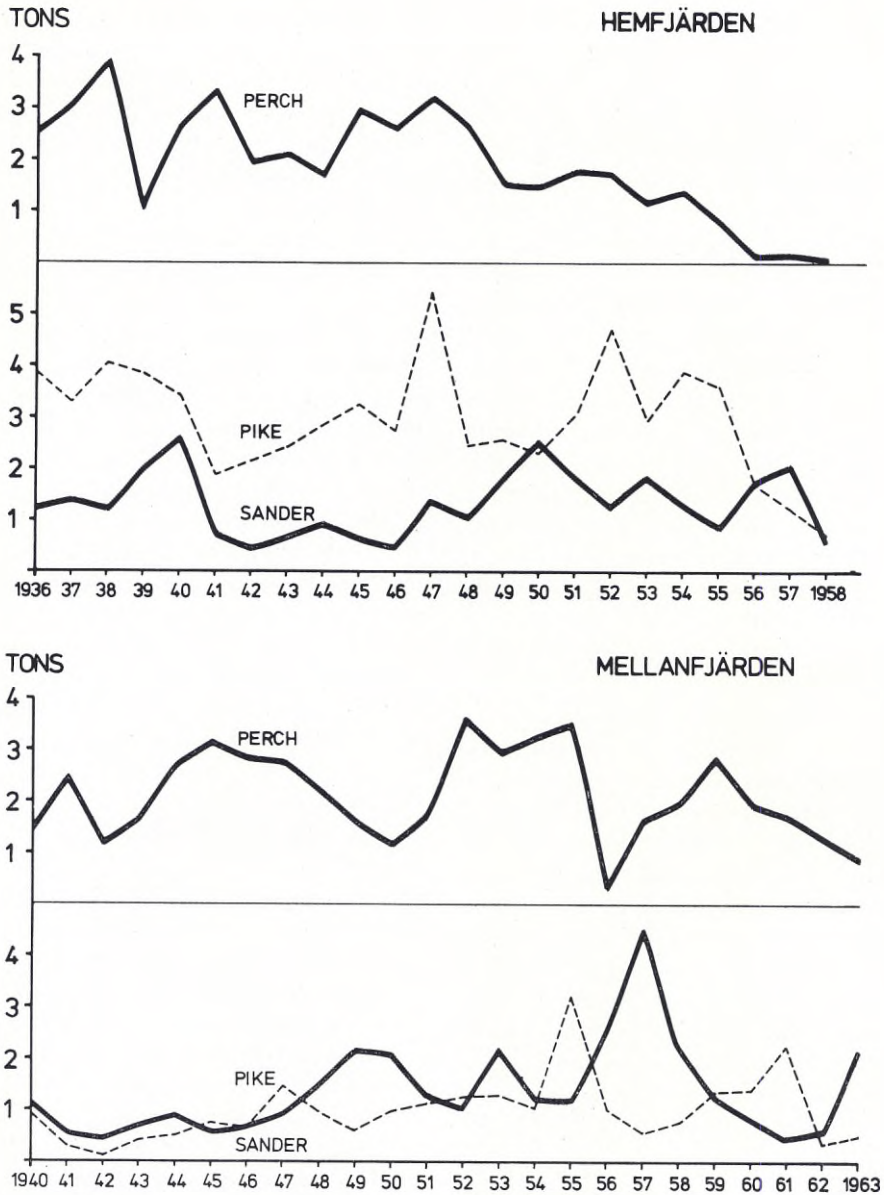


Fig. 15. Catch records from two commercial fishermen on Lake Hjälmaren.

should decrease according to the long term change of summer temperatures.

The growth analyses, reported in an earlier section, indicate that the sander of Lake Hjälmaren were overexploiting their food supply in early or mid 60's, but that this food supply has later recovered. In Lake Mälaren, a parallel but less

pronounced growth rate change occurred. With the exception of the smelt, our gill nets also registered the potential forage species taken together with the sander (Tables 8 and 9). Roach, white bream and bream all peaked in Lake Hjälmaren in 1966—67, 1967—69 and 1971—72, respectively, which confirms that a less intense

Table 8. Total catch (numbers) at the Mellanjärden fishing station, Lake Hjälmaren 1955—1972, not adjusted to slightly fluctuating effort during the first years.

	<i>Stizostedion lucioperca</i>	<i>Esox lucius</i>	<i>Percu fluviatilis</i>	<i>Abramis brama</i>	<i>Blicca bjoerkna</i>	<i>Rutilus rutilus</i>	<i>Scardinius erythrophthalmus</i>	<i>Carassius carassius</i>	<i>Abramis ballerus</i>	<i>Aspius aspius</i>	<i>Timca tinca</i>	<i>Lota lota</i>
1955	36	32	18	123	125	8	6	2	—	3	1	4
1956	136	9	33	182	301	19	1	—	—	—	—	2
1957	74	4	45	63	152	5	—	—	—	—	—	—
1958	63	5	163	132	114	18	—	—	—	—	—	—
1959	72	12	139	119	71	5	4	—	2	—	—	1
1960	44	9	16	67	62	2	—	—	—	—	—	—
1961	38	1	30	106	200	18	1	2	—	—	—	—
1962	44	6	15	70	85	9	—	—	—	1	—	—
1963	99	2	12	219	216	17	—	—	—	1	—	—
1964	109	1	34	319	233	26	3	—	—	—	—	—
1965	69	6	28	192	515	126	2	—	—	—	—	—
1966	121	6	128	175	572	308	—	—	—	—	—	—
1967	51	6	117	189	835	402	17	—	—	1	—	—
1968	133	9	182	318	893	181	—	—	5	—	—	—
1969	123	4	37	113	1059	43	—	—	2	—	—	1
1970	96	5	11	173	447	56	—	—	2	1	—	—
1971	92	8	13	372	409	26	—	—	3	1	—	—
1972	88	—	8	988	631	46	—	—	2	—	—	—

Table 9. Total catch at the Lambarfjärden fishing station, Lake Mälaren 1955—1972, not adjusted to effort in the first few years.

	<i>Stizostedion lucioperca</i>	<i>Esox lucius</i>	<i>Percu fluviatilis</i>	<i>Abramis brama</i>	<i>Blicca bjoerkna</i>	<i>Rutilus rutilus</i>	<i>Coregonus albula</i>	<i>Lota lota</i>	<i>Coregonus lavaretus</i>	<i>Abramis ballerus</i>	<i>Myoxocephalus quadricornis</i>
1955	33	10	44	76	4	—	—	44	1	—	—
1956	25	4	3	74	11	—	2	80	—	1	10
1957	96	6	21	194	33	3	—	64	—	—	1
1958	88	5	31	89	10	13	6	65	3	—	11
1959	95	7	73	72	57	13	74	13	4	—	1
1960	138	4	26	78	38	24	80	35	11	—	—
1961	145	—	62	70	18	6	101	29	4	—	5
1962	67	2	38	26	14	—	70	10	—	—	—
1963	97	3	57	100	32	55	36	31	—	—	—
1964	77	3	120	57	24	—	27	36	—	—	—
1965	52	—	138	28	2	—	93	61	—	—	—
1966	45	3	236	78	23	—	142	22	1	—	—
1967	46	6	61	47	21	—	347	85	—	—	—
1968	412	5	209	61	58	—	312	88	1	—	—
1969	303	2	20	100	83	304	87	46	3	—	—
1970	204	4	153	39	30	79	124	45	—	—	—
1971	105	2	82	33	41	—	350	43	2	—	—
1972	208	2	77	46	41	19	305	68	—	—	—

sander predation may have contributed to their population increase.

No parallel increase of the same species has occurred in Lake Mälaren. The increase of the cisco (Table 9) may be biased as is the sander catch.

VII. DISCUSSION

There is a general experience from hatchery work on salmon and trout that the winter losses may be severe if the fingerlings are too short or, to put it more accurate, too thin.

In a warm water species, like carp, which was formerly cultivated in larger numbers in Sweden than now, the size of the summer-old fish is decisive for the winter loss. It was found that the northernmost limit for rearing carp in Sweden was dependent on the summer climate. If the summer was too short or cold, the young carp could not stand the stress of the winter.

FORNEY (1966) found that the walleye of Oneida Lake, N.Y. apparently increased in size between samples in late autumn and early spring. The scales did not indicate growth, however, and the 20 mm increase in average size was most probably due to size-selective mortality during the winter. The dominant year class of 1959 was correlated to larger than usual size of the autumn-sampled young walleye in Oneida Lake (FORNEY 1966), Black Lake (LE TENDRE and SCHNEIDER 1969), Winnebago Lake (PRIEGEL 1970) and Pike Lake (MRÄZ 1968).

In his significant yellow perch study, FORNEY (1971) again found three dominant year classes to be represented by heavier than average perch in the autumn. The index for year class strength rose sharply in the winter, indicating a depensatory mortality which killed a smaller proportion of the more dominant classes.

CHRISTIE and REGIER (1973) discussed warm summers' growth and winter mortality of the smallmouth bass.

KIPLING and FROST (1970) found dominant pike

year classes correlated to first year growth and number of degree days over 14°C. Yearling pike below 20 cm were supposed to be preyed on by larger pike during the first winter.

BIRÓ (1972) found an apparent growth of Lake Balaton 0+ sander from September—October to May of about 5 cm indicating heavy first winter losses of the small fingerlings (6—9 cm) of this population. A decrease of condition was also noted in spring. NEGONOVSKAYA (1972) also noted an apparent increase of size of underyearling sander during the first winter. She relates this phenomenon to a possibly greater mortality of the smallest specimens.

More evidence come from the failures to produce better yield by releasing fingerling sander or walleye in late summer (RAHN 1958, TESCH 1961, MRÄZ 1968, NEGONOVSKAYA 1972, KEMPINGER and CHURCHILL 1972). ALM (1961) three times released young sander in a small lake near the Kälärne hatchery station but not one single sander was caught. Young sander have repeatedly been put into Lake Siljan (290 km²) but only a very few adult fish have been recovered, in spite of abundant food like smelt and small-sized cisco. The experience is similar in a score of northern Swedish lakes, suggesting a very high first winter mortality.

Apart from the selective mortality caused by predators there seem to be a similar size-dependent mortality which is possibly related to the amount of fat that the young fish may deposit in autumn. KELSO (1973) found the energy content of walleye to drop from autumn to spring and increase in summer.

The warmer the summer, the larger the size attained by the 0+ sander and the better the odds to survive until next spring. Since temperature sums tend to fluctuate above or below average in a parallel way within the same climatic zone, the first winter mortality actually may be the real factor behind synchronous year classes.

The six Swedish lakes studied in this paper, can be arranged in the following order:

	Sander yield, kg/km ²	Con- ductivity	pH	Total-P	Trans- parency	Strati- fied
Lake Vombsjön	213—700	371	8.9	90	1	no
Lake Hjälmaren	202—508	193	7.8	46	2	no
Lake Mälaren	79—167	138	7.5	36	3	yes
Lake Ivösjön	5— 28	120	7.3	15	4	yes
Lake Vänern	11— 20	70	6.9	12	4	yes
Lake Orsjön	11	30	7.1	12	4	yes

Table 10. Fish population on two sander spawning grounds, Lake Vänern.

Species	Dettern Bay		Varnums Bay, Kristinehamn	
	8—19 May 1972	15—19 May 1973	1—6 June 1972	4—9 June 1973
<i>Rutilus rutilus</i>	900	496	464	182
<i>Abramis brama</i> / <i>Blicca bjoerkna</i>	790	331	299	201
<i>Gymnocephalus cernua</i>	641	396	352	233
<i>Stizostedion lucioperca</i>	109	20	10	6
<i>Perca fluviatilis</i>	91	57	324	158
<i>Abramis ballerus</i>	63	188	2	—
<i>Alburnus alburnus</i>	8	63	126	7
<i>Aspius aspius</i>	2	2	—	—
<i>Lota lota</i>	1	1	—	—
<i>Osmerus eperlanus</i>	1	—	3	2
<i>Esox lucius</i>	—	6	4	4
<i>Leuciscus idus</i>	—	2	—	—

The favourable sander habitat, as judged from this table, conforms to the result reported elsewhere. JÄRNEFELT (1949) found the sander lakes of the Vanjavesi river in Finland to have a transparency of two metres or less in 93 % of the cases (43 lakes). The average depth was low, suggesting no stratification. TOIVONEN (1965) pointed out that eutrophication by organic waste waters favoured the sander habitats. Low temperature and oxygen deficiencies hampered the spread of the species. In Poland, MIKULSKI (1964) found the sander lakes to be shallow, have transparency less than one metre, to be wind-swept, homothermic and with a plankton fauna dominated by *Rotatoria* and *Daphnia cucullata*. He also found sander production strongly related to the content of organic matter (B.O.D.), up to 8 mg O₂/l, while sander introductions had failed in lakes with B.O.D. as low as 1.0—1.3.

Both sander and walleye are dependent on oxygenated bottoms, probably for daytime rest (REGIER *et al.* 1969). OSEID and SMITH (1971) found walleye fry to be some ten per cent smaller when hatched in water with 2 ppm oxygen. Whatever the reason, the sander thrive in a homothermic lake, as evidenced by the lakes Vombsjön and Hjälmaren.

The richer year classes (more dense population) in eutrophic lakes may predominantly be related to better growth rate and better survival of fry in the turbid water.

As mentioned before, the decline of sander in Lake Vänern, was probably due to organic pollution according to the commercial fishermen. It has already been pointed out that the climate seems a more reasonable cause. Moreover, the reaction of the sander in the oligotrophic Lake Bolmen (183 km²) and Lake Vättern (1,899 km²) is of interest. In both lakes sander has been recently introduced and the species has concentrated in the northernmost bays of both lakes, which happens to be the parts of the lakes which are most turbid and enriched by organic matter.

Competition may hamper the sander growth during the first summer (*cf.* BIRÓ 1972) and thereby cause the first winter loss to be higher. Some test fishing was done at the most important spawning areas in Lake Vänern. The coarse fish fauna was impressive (Table 10). The abundant roach may be a serious competitor, as SUMARI (1971) found the roach capable of reducing the standing crop of perch in small lakes to fractions only. TÄGTSTRÖM (1937, 1938) reported from his pond-rearing experiments with the sander that the young became stunted by whitefish fry competition. Perch fry, which "contaminated" the water intake of the ponds, competed with sander and stunted their growth and in late summer the largest perch became predacious on sander and exterminated them. MUKHACHEV (1971) stressed the slow increase of the sander stock when introduced into a lake with abundant perch. NEGO-

NOVSKAYA (1971) found sander fry in the stomachs of perch and ruffe on the sander spawning grounds.

It should be noted that the walleye/yellow perch relation in North America during their first summer is not quite equal to the sander/perch relation in Europe, because of the later spawning period of the sander compared to that of the walleye. NEGONOVSKAYA (1972) stressed that 1+ sander prey on 0+ perch in Lake Pskov-Chudskoye.

Speculatively, there might be a stage of organic enrichment where the coarse fish fauna has increased because of more reeds or dense littoral vegetation while the turbidity is still modest. That could mean more food competition for the young sander, slower growth and hence lower survival and possibly a stronger predation pressure on the sander as well. If there be such a transitory stage in the enrichment process, however, the sander is no doubt favoured at higher levels of enrichment, as evidenced by the practical experience from several countries.

If the size after the first summer's growth is the decisive factor for winter survival then there would be a selective pressure favouring earliest possible spawning, other things being equal. It is an interesting fact that the Dettern bay of Lake Vänern and the lower Arbogaån river of Lake Mälaren are the only spawning grounds known, where sander may regularly spawn already in the last week of April. Both stocks also seem to be the densest known in the whole country. The sander of these local stocks migrate a considerable distance to their fattening areas, proved by tagging for one of them. The first winter mortality thus not only interferes with the geographical distribution of the species and the abundance in different environments but has also moulded, by natural selection, some of the ecological characters of the sander.

VIII. IMPLICATIONS FOR MANAGEMENT

The evidence obtained in this study on the population phenomena of the sander should have some consequences for the management of this valuable species.

The era of early fry release is gone. That of

one-summer-old sander has also culminated, not so much because of lacking belief of those selling the fingerlings, but of those purchasing them. The price is very high, and to judge from the percentage recoveries known from abroad (1—13 %), a sander of hatchery origin may cost some 10—50 Swedish crowns.

Climate cannot be manipulated and the organic pollution is defeated by all means, including new laws and the building of numerous sewage treatment plants. The water of Lake Mälaren has become more transparent in the last few years and in 1973 a public out-of-door bathing site was opened within the Stockholm city area.

There remains some possible means of promoting the sander habitat. Water levels often cannot be manipulated but, locally on sander spawning grounds, it might be possible to increase the turbidity on clay bottoms by mechanical means during a period from early May to June. This type of management, however, certainly will not cause general approval.

The competitive pressure exerted by the coarse fish fauna might be reduced by fishing operations. The economy of this activity remains to be solved, since there is no market for the fish landed. In Lake Vombsjön a local commercial fisherman has exploited his huge coarse fish landings for trout farming operations and, as it seems, he has promoted his sander population at the very same time.

Since the adult sander is capable of making heavy inroads into the competitive fish fauna, thereby favouring the survival of its own progeny, the most promising management would be to allow the sander to live one or two years longer than is now the case. The average total mortality, as judged by the scale readings, is some 50 per cent and only a small minority of the growing sander become mature. Overfishing is most often discussed in numbers of eggs or fry but should perhaps be discussed in numbers of adult predators on the fry-competing species also (cf. REGIER *et al.* 1969).

Moreover, overfishing means an intense selection for early maturity. Like all kinds of strong artificial selection it may produce correlated responses, producing fish of lower fitness.

Sander as well as walleye (PARSONS 1971) have proved to be capable of producing a dominant

year class from very few parental fish. This fact should not be used as an argument for excluding closed seasons, reduction of gill net numbers and using larger mesh sizes from the manager's tools.

IX. SUMMARY

Six Swedish sander lakes are described and the yield discussed. Two of the lakes are excellent sander habitats, one very unfavourable and the remaining three intermediate ones, including the largest lake of Scandinavia, Lake Vänern.

Year classes were studied in two lakes, *i.e.* Lake Hjälmaren and Lake Mälaren, by fishing fixed localities, with a constant set of gill nets and efforts, over the period 1955—72. The fifteen year classes 1953 through 1967 could be scored in both lakes and were found to fluctuate in a similar way, indicating climatic influence.

The score of the year class was significantly correlated to the temperature of some summer months, above all the period June—August.

When the regression of year class strength on air temperature was used in two other lakes, the calculated catchable sander populations ran parallel to the known yield.

Some evidence was obtained that high water level in spring may add to the strength of a year class.

Growth rates are given for the sander of the six lakes. Females grow slightly better than males from their sixth year in Lake Mälaren. The sex ratio is even. Growth is better in warm years, especially for small fish. Population density interferes with growth rate when it is high. There were simultaneous growth rate fluctuations in Lake Hjälmaren and Lake Mälaren, but they were more pronounced in the first lake. Forage fish fauna was reduced in those years.

The interaction between sander, pike and perch is most obvious when sander is introduced into new lakes but can be traced at high population levels in other lakes also.

The ultimate factor creating dominant year classes in Scandinavian sander is suggested to be first winter mortality. Anything promoting growth, like higher organic production of lakes, higher than average temperature during a certain year,

fewer competitive other fish, or the access to spawning grounds permitting unusually early spawning, may all be favourable for the sander. The implications for management are discussed.

X. ACKNOWLEDGMENTS

The authors are grateful to fishery consultants BRODDE ALMER and HUGO RUNDBERG for material and most valuable information on Lake Vänern and Lake Ivösjön (ALMER) and Lake Mälaren and Hjälmaren (RUNDBERG). Fishery consultants C. G. HAMMARLUND, T. LARSSON, G. SVENSSON and H. WIEDERBERG also kindly supplied information.

XI. REFERENCES

- AGNEDAL, P.-O. 1969. Studier av abborre och fiskets avkastning i Erken. 64 p. (Mimeographed in Swedish.)
- AHL, T. 1971. Tillfriskning av recipienter, tidigare belastade med avloppsvatten från sulfidfabriker — Arbogaån. *IVL-publikation A65:96—110*. (Mimeographed in Swedish.)
- ALM, G. 1917. Undersökningar rörande Hjälmarens naturförhållanden och fiske. *Medd. K. Landtbr. Styr.* 3(204):1—111. (In Swedish, German summary.)
- 1936. Huvudresultaten av fiskeribokföringsverksamheten. *Rep. Inst. Freshw. Res. Drottningholm* 11. 64 p. (In Swedish, German summary.)
- 1961. Die Ergebnisse der Fischeausätze in den Kälarne-Seen. *Rep. Inst. Freshw. Res. Drottningholm* 42:5—83.
- ALMER, B. 1971. Ivösjön under den senaste 100-årsperioden. *Limnol. Inst. Uppsala*. 28 p. (Mimeographed in Swedish.)
- ÄNGSTRÖM, A. 1946. Sveriges klimat. Generalst. lit. anst. Stockholm 105 p. (In Swedish.)
- ARWIDSSON, I. 1904. Gösen i sjön Valloxen i Uppland. *Svensk Fisk. Tidskr.* 13(1):30—31. (In Swedish.)
- BANARESCU, P. *et al.* 1971. European Inland Water Fish. Publ. FAO by Fishing News Ltd Books, London.
- BELLY, N. D. 1968. Behavior and settling of free pike-perch (*Lucioperca lucioperca* L.) embryos hatching out in deep water. *Probl. Ichthyology* 8(5):712—718.
- BIRÓ, P. 1972. First summer growth of pike-perch (*Lucioperca lucioperca* L.) in Lake Balaton. *Ann. Biol. Tibany* 39:101—113.
- CHRISTIE, W. J. 1973. A review of the changes in the fish species composition of Lake Ontario. *Tech. Rep. Gr. Lakes Fish. Comm.* 23. 65 p.

- and H. A. REGIER 1973. Temperature as a major factor influencing reproductive success of fish — two examples. Fish stocks and recruitment. *Rapp. Cons. Explor. Mer* 164: 208—218.
- DAHL, J. 1962. Bedeutung und Ertrag der Zanderfischerei in der Bewirtschaftung dänischer Seen. *Z. Fisch. X. N.F.* (8/10): 689—695.
- DEELDER, C. L. and J. WILLEMSSEN. 1964. Synopsis of biological data on pike-perch, *Lucioperca lucioperca* (LINNAEUS) 1758, FAO Fish. Biol. Synops. 28, 62 p.
- EKMAN, S. 1922. Djurvärdens utbredningshistoria på den skandinaviska halvön. Bonniers, Stockholm. 612 p. (In Swedish.)
- ELROD, J. H. and TH. J. HASSLER 1969. Estimates of some vital statistics of northern pike, walleye, and sauger populations in Lake Sharpe, South Dakota. *Tech. Pap. Bur. Sport. Fish. Wildl.* 30. 18 p.
- ESCHMEYER, P. H. 1948. The life history of the walleye (*Stizostedion vitreum vitreum* (MITCHILL)) in Michigan. *Bull. Inst. Fish. Res. Univ. Mich.* 3. 99 p.
- FORNEY, J. L. 1966. Factors affecting first-year growth of walleyes in Oneida Lake, New York, N.Y. *Fish Game J.* 13(2): 146—167.
- 1971. Development of dominant year classes in a yellow perch population. *Trans. Amer. Fish. Soc.* 100(4): 739—749.
- FREIDENFELT, I. 1922. Undersökningar över gösens tillväxt särskilt i Hjälmaren. *Medd. K. Lantbr. Sty.* 235: 1—75. (In Swedish, German summary.)
- FROMM, E. 1953. Nedisning och landhöjning under kvartärtiden. Atlas över Sverige. p. 19—20. Generalst. lit. anst. Stockholm. (In Swedish.)
- HANKO, B. 1932. Ursprung und der Verbreitung der Fishfauna Ungarns. *Arch. Hydrobiol.* XVIII: 520—556.
- HILE, R. 1954. Fluctuations in growth and year-class strength of the walleye in Saginaw Bay. *Fish. Bull. Fish. Wildl. Serv. U.S. Dep. Int.* 91. 59 p.
- JÄRNEFELT, H. 1949. Die Fische und die Gewässertypen. *Verh. int. Ver. Limnol.* X: 216—231.
- KELSO, J. R. M. 1973. Seasonal energy changes in walleye and their diet in West Blue Lake, Manitoba. *Trans. Amer. Fish. Soc.* 102(2): 363—368.
- KEMPINGER, J. J. and W. S. CHURCHILL 1972. Contribution of native and stocked walleye fingerlings to the angler's catch, Escanaba Lake, Wisconsin. *Trans. Amer. Fish. Soc.* 101(4): 644—649.
- KIPLING, C. and W. E. FROST 1970. A study of the mortality, population numbers, year class strengths, production and food consumption of pike, *Esox lucius* L., in Windermere from 1944 to 1962. *J. Anim. Ecol.* 39: 115—157.
- KLEINERT, S. J. and P. E. DEGURSE 1968. Survival of walleye eggs and fry of known DDT residue levels from ten Wisconsin waters in 1967. *Res. Rep. Dep. Nat. Res. Wisc.* 37. 30 p.
- LARKIN, P. A., J. G. TERPENNING and R. R. PARKER 1956. Size as a determinant of growth rate in rainbow trout, *Salmo gairdneri*. *Trans. Amer. Fish. Soc.* 86: 84—96.
- LAWLER, G. H. 1965. Food of the pike, *Esox lucius*, in Heming Lake, Manitoba. *J. Fish. Res. Bd. Canada* 22(6): 1357—1377.
- LECREN, E. D. 1958. Observations on the growth of perch (*Perca fluviatilis* L.) over twentytwo years with special reference to the effects of temperature and change in population density. *J. Anim. Ecol.* 27: 287—334.
- LETENDRE, G. C. and C. P. SCHNEIDER 1969. Age and growth of male walleyes in spawning runs from Black Lake, New York, N.Y. *Fish Game J.* 16(2): 136—144.
- LÖNNBERG, E. 1898. Notizen über das Vorkommen des Zanders in Schweden. *Fischerei Ztg Neudamm* 1(50): 796—799.
- MÄÄR, A. 1947. Om gösens tillväxt i bräckt och sött vatten. *Skr. S. Sverig. Fisk. Fören.* 1947(1): 6—15. (In Swedish, German summary.)
- MIKULSKI, J. S. 1964. Some biological features of perch-pike lakes. *Verh. int. Ver. Limnol.* XV: 151—157.
- MRAZ, D. 1968. Recruitment, growth exploitation and management of walleyes in a southeastern Wisconsin Lake. *Tech. Bull. Dep. Nat. Res. Wisc.* 40. 38 p.
- MUKHACHEV, I. S. 1971. The rate at which the perch (*Perca fluviatilis*) populates lakes. *J. Ichthyology* 11(3): 421—423.
- MUNTYAN, S. P. 1966. Effect of constant incubation temperatures on the hatching process and on the morphological characters of pike-perch embryos. Rep. All-Union. Conf. Ecol. Physiol. Fishes, Moscow.
- NEGONOVSKAYA, I. T. 1971. Conditions of natural reproduction of the pike-perch (*Lucioperca lucioperca* (L)) in Lake Pskov-Chudskoye. *J. Ichthyology* 11(4): 630—635.
- 1972. Data on the food of younger age groups of the pike-perch *Lucioperca lucioperca* (L.) in Lake Pskov-Chudskoye. *J. Ichthyology* 12(3): 473—482.
- NIKOLSKI, G. W. 1957. Spezielle Fischkunde. Deutsch. Verlag Wiss. Berlin. 632 p.
- NORDQVIST, H. 1931. Södra Sveriges Fiskeriförenings insjöfiskeförsök. *Skr. S. Sverig. Fisk. Fören.* 1931(1): 16—54. (In Swedish.)
- NORDQVIST, O. 1905. Om gösen och gösodling. *Svensk Fisk. Tidskr.* 14(1): 86—95. (In Swedish.)
- 1906. Anteckningar om gösens levnadsförhållanden och gösfisket i Dettarn. *Svensk Fisk. Tidskr.* 15(1): 6—13. (In Swedish.)
- OLSON, D. E. 1968. Sex ratios of young-of-year walleyes in Minnesota rearing ponds and lakes. *Progr. Fish Cult.* 30(4): 196—202.
- OSEID, D. M. and L. L. SMITH 1971. Survival and hatching of walleye eggs at various dissolved oxygen levels. *Progr. Fish Cult.* 33(2): 81—85.
- PARSONS, J. W. 1971. Selective food preferences of walleye of the 1959 year class in Lake Erie. *Trans. Amer. Fish. Soc.* 100(3): 474—485.

- PRIEGEL, G. R. 1970. Reproduction and early life history of the walleye in the Lake Winnebago region. *Tech. Bull. Dep. Nat. Res. Wisc.* 45: 105 p.
- PUKE, C. 1952. Pike-perch studies in the Lake Vänern. *Rep. Inst. Freshw. Res. Drottningholm* 33: 168—178.
- RAHN, J. 1958. Über Möglichkeiten und Grenzen der Steigerung des Feinfischertrages unserer Seen- und Flussfischerei durch Besatzmassnahmen. *Dtsch. Fisch.-Ztg.* 2: 42—49.
- RAWSON, D. S. 1957. The life history and ecology of the yellow walleye, *Stizostedion vitreum* in Lac La Ronge, Saskatchewan. *Trans. Amer. Fish Soc.* 86: 15—37.
- REGIER, H. A., V. C. APPLGATE and R. A. RYDER 1969. The ecology and management of the walleye in western Lake Erie. *Tech. Paper Gr. Lakes Fish. Comm.* 15: 101 p.
- RITZANOV, R. A. 1970. The spawning biology of the Lake Ladoga pike-perch (*Lucioperca lucioperca* L.). *J. Ichthyology* 10(5): 619—625.
- RUNDBERG, H. 1968. Fisket i Mälaren. *Inform. Inst. Freshw. Res. Drottningholm*. 13. 48 p. (Mimeographed in Swedish.)
- 1971. Fisket i Hjälmaren. *Inform. Inst. Freshw. Res. Drottningholm*. 13. 27 p. (Mimeographed in Swedish.)
- SEGERSTRÅLE, C. 1936. Fiskeribiologiska undersökningar rörande gösen. (*Lucioperca sandra* Cuv.) i östligaste delen av Finska Viken. Nord. 19 naturforskmötet i Helsingfors. p. 500—506. (In Swedish.)
- 1947. Fiskodling och fiskevård. Helsingfors. 240 p.
- SMITH, L. L. and R. L. PYCHA 1961. Factors related to commercial production of the walleye in Red Lakes, Minnesota. *Trans. Amer. Fish. Soc.* 90(2): 190—217.
- SUMARI, O. 1971. Structure of the perch populations of some ponds in Finland. *Ann. Zool. Fennici.* 8(3): 406—421.
- SVÄRDSON, G. 1948. Ett gösmärkningsförsök. *Svensk Fisk. Tidskr.* 57(11): 173—174. (In Swedish.)
- 1972. The predatory impact of eel (*Anguilla anguilla* L.) on the populations of crayfish (*Astacus astacus* L.). *Rep. Inst. Freshw. Res. Drottningholm* 52: 149—191.
- and G. MOLIN 1968. Growth, weight and year-class fluctuations in the pike-perch (*Lucioperca lucioperca* L.) of Lakes Hjälmaren and Mälaren. *Rep. Inst. Freshw. Res. Drottningholm* 48: 17—35.
- TÄGTSTRÖM, B. 1937. Erfarenheten vid odling av sik och gös i dammar. *Svensk Fisk. Tidskr.* 46(3): 53—58, (6): 153—157. (In Swedish.)
- 1938. Redogörelse till Kungl. Lantbruksstyrelsen för försöksverksamheten vid Harviks Fiskodling år 1938. *Svensk Fisk. Tidskr.* 47(12): 329—332. (In Swedish.)
- TESCH, F. W. 1955. Das Wachstum des Barsches (*Perca fluviatilis* L.) in verschiedenen Gewässern. *Z. Fisch.* IV. N.F.: 321—420.
- 1959. Die Zanderlaichverhältnisse (*Lucioperca lucioperca* L.) auf Grund von Laichnestkontrollen im Müggelsee. *Z. Fisch.* VIII (7/8). N.F.: 587—596.
- 1961. Über die Rentabilität des Einsatzes von Zandersetzlingen (*Lucioperca lucioperca* L.) in den Bülzsee. *Dtsch. Fisch.-Ztg.* 8(5): 135—137.
- 1962. Witterabhängigkeit der Brutentwicklung und der Nachwuchsförderung bei *Lucioperca lucioperca* L. *Kurz. Mitt. Inst. Fischbiol. Univ. Hamb.* 12: 37—44.
- 1965. Wie Zander und Blei den Barschbestand verdrängen. *Allg. Fisch. Ztg.* 90(24): 126—128.
- TIDEMAN, M. 1933. Några anteckningar från gösfisket i Östergötlands län. *Svensk Fisk. Tidskr.* 42(1): 3—5. (In Swedish.)
- TOIVONEN, J. 1965. Pikeperch and the eutrophication of the lakes in Finland. Limnologisymposion, Helsingfors 1965: 62—67. (In Finnish, English summary.)
- 1969. Gösmärkning på Åland. *Medd. Husö biol. stat.* 14: 16—23. (In Swedish.)
- TÖRNQVIST, N. 1941. Fiskets avkastning i Vänern. *Svensk Fisk. Tidskr.* 50(6): 129—134. (In Swedish.)
- UGGLA, HILLEBRANDSSON 1786. Inträdes-Tal om sjön Hjälmaren, hållet för Kongl. Vetenskaps Akademien den 9 augusti 1786. J. George Lange, Stockholm. 32 p. (In Swedish.)
- VALLIN, S. 1929. Sjön Ymsen i Skaraborgs län. *Medd. K. Lantbr. Styr.* 277: 1—43. (In Swedish, German summary.)
- WIEDERBERG, H. 1941. Kan gösodlingen förenklas? *Svensk Fisk. Tidskr.* 50(8): 175—178, (9): 193—198, (10): 218—221. (In Swedish.)
- 1967. Mälaren och Hjälmaren. Uppgifter över fiskfångster m.m. inom Västmanlands län under åren 1923—1966. (Mimeographed in Swedish.)
- WILLÉN, T. 1972. Biological aspects on the large lakes in South Sweden. *Verh. int. Ver. Limnol.* 18: 370—378.
- ZAWISZA, J. and T. BACKIEL 1972. Some results of fishery biological investigations of heated lakes. *Verh. int. Ver. Limnol.* 18: 1190—1197.

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