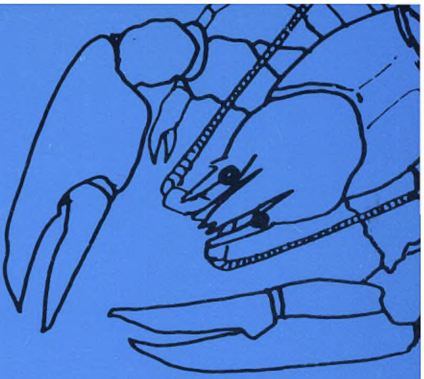

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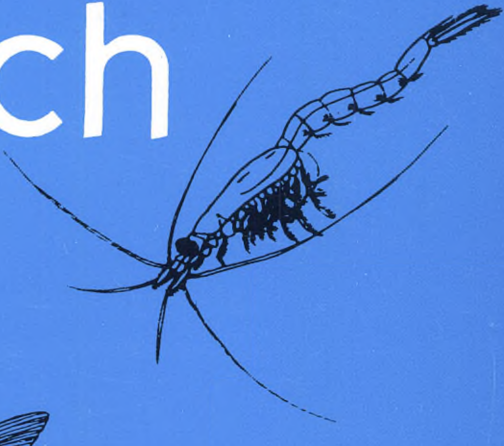

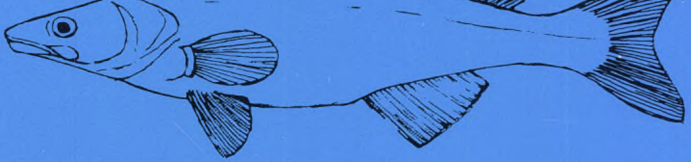

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The Crustacean Plankton and Fish in a Subalpine Reservoir Subject to Oxygen Deficiency

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Abstract

The Finnkojsjø reservoir in Central Norway was made in 1970 by flooding 6.20 km^2, mainly bogs and wetland. At lowest water level, its area is 1.62 km^2 and its mean depth 0.7 m. From 1973, an increasing smell of H_2S has been noticed in winter from the water leaving Finnkojsjø. During 1969–79, its crustacean plankton changed from a predominantly cladoceran to an almost completely diaptomid community. Its population of Arctic char died out in 1973, a consequence of the lack of spawning grounds. Until 1973 inclusive, its population of brown trout was comparable with those of other Norwegian impoundments as regards catch per effort, growth and condition factor. By 1979, the trout had also disappeared; this is connected with the anaerobic conditions in winter.

Introduction

The production of certain invertebrates and fish is usually high in impoundments, especially during the early years (Mordukhai-Boltovskoi et al. 1972, Baxter 1977, Baxter and Glaude 1980).

The Nesjø and Finnkojsjø hydroelectric impoundments were made in the counties of Trøndelag, Norway in 1970 (Fig. 1). The distance between them is 11 km and their altitudes differ by 40 m. In both cases the flooded areas were mainly bogs and wetland. The Nesjø reservoir covering 38.7 km^2 and with maximum depth 30 m, has a highest water level of 729.0 m a.s.l. At 722.4 m it

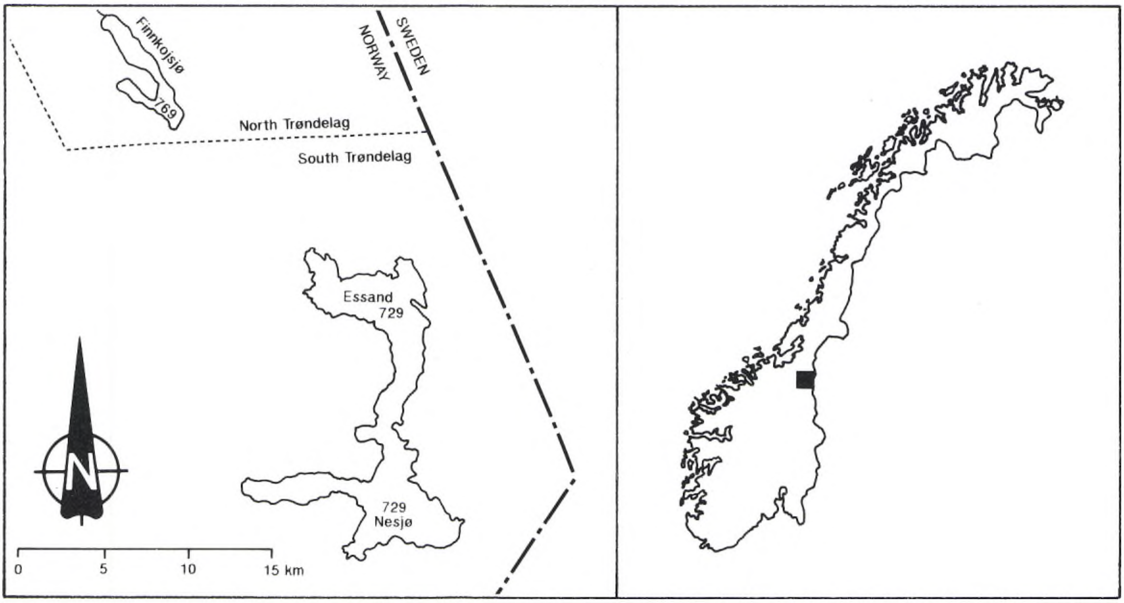

Fig. 1. Map of the research area with the reservoirs.

Table 1. Characteristics of the Finnkojsjø reservoir.

Water level	Altitude m	Volume m^3	Areal km^2	Mean depth m
Highest	769	$44.85 * 10^6$	6.20	7.2
Lowest	758	$1.15 * 10^6$	1.62	0.7

is connected to the 27.3 km^2 large Essand reservoir, made in 1947. This system was a success with respect to fish production, and during its first 13 years it was known to have the best lake fishing for salmonids in Scandinavia (Jensen 1988).

As regards fish, the other impoundment, Finnkojsjø, became a failure. Its populations of brown trout (*Salmo trutta* L.) and Arctic char (*Salvelinus alpinus* (L.)) had both died out by 1979. This paper deals with the crustacean plankton and fish in Finnkojsjø and the factors causing their negative development. It emphasizes the contrasts between the Nesjø and Finnkojsjø reservoirs.

The Finnkojsjø reservoir

Finnkojsjø was constructed in 1970 by damming the River Lødølja and flooding the small Lake Gåstjern. The difference between its highest and lowest water level is 11 m (Table 1). At its lowest level the mean depth is only 0.7 m and the maximum depth about 2 m.

Bogs and wetland represented 60–70 % of the flooded area. It included 8 km of the River Lødølja and the Lake Gåstjern of area 0.45 km^2 and maximum depth 10 m (Fig. 2). The river was slow flowing and had limited areas favourable for juvenile brown trout. Gåstjern was populated by brown trout and Arctic char.

The reservoir was operated on a regular regime during the research period. Water was stored in April–September and drained in winter until May. Except in 1977 the water was at, or close to, the designed maximum level every summer. In the winter of 1971–73 and 1978 the water was left 3.8 to 5.1 m above the lowest level, 758 m (Fig. 3). In 1975–77 and in 1979 the reservoir was lowered to 758 m.

Material and methods

Data were collected in June 1969, autumn 1970, July 1971, September 1973, June and September 1977 and four times in 1979. Additional hydrographical data are given by Heggstad (1974, 1980). Crustacean plankton was sampled by vertical hauls from bottom to surface using a nylon net

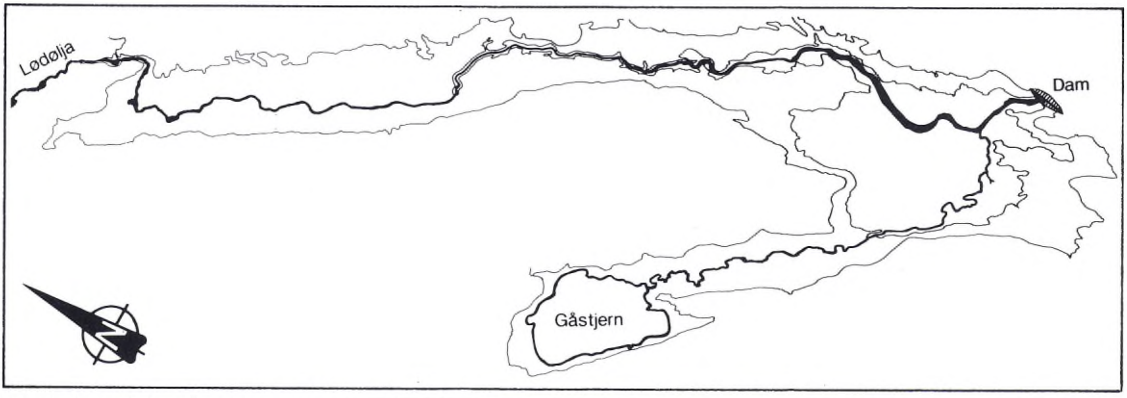

Fig. 2. Map of the Finnkojsjø reservoir with highest and lowest water levels permitted, and the original water system (thick line), scale 1 : 50,000.

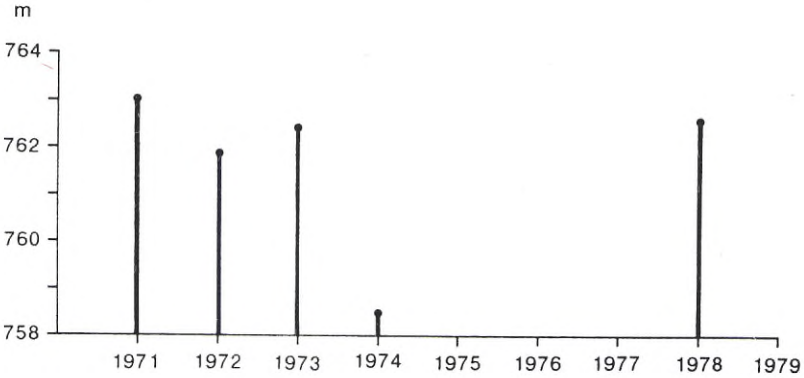

Fig. 3. The minimum water levels in the Finnkojsjø main basin in 1971–79.

of mesh size 90 μm, mouth diameter 29.0 cm and length 100 cm. When testing this net in Nesjø, Jensen (1988) found a net factor of 2.0 for sum Crustacea with confidence limits of 1.8 and 2.3 ($P<0.05$). For nets of similar specifications net factors between 1.7 and 1.9 have been recorded (Patalas 1954, Prepas and Rigler 1978, Jensen 1982, Koksvik and Arnekleiv 1988). Consequently, the numbers caught were multiplied by 2. On each occasion in 1979, 4 hauls were taken in the Gåstjern basin and 7 in the remaining parts of the reservoir (in the following sections called the main reservoir). Otherwise, two replicate hauls were taken at each location. The precision of the 1979 means is generally within ±40–50 % ($P<0.05$).

The body length of the first 30 randomly occurring individuals of the cladoceran species in each sample was measured. The body length of the different stages of the copepod species was measured in 1979. Mean dry weights in μg were calculated from mean body lengths according to equations given by Bottrell et al. (1976), Larsson (1978), Langeland (1982), all quoted by Jensen (1988).

Macrobenthos was sampled at 3 locations in Gåstjern in 1969. 5 probes were taken at each m depth from 1 to 7 m with a van Veen sampler covering 0.02 m^2, pooled and sieved through 0.5 mm mesh. The sampling was repeated in 1971 at the same locations.

Fish were caught using series of nylon twine gill nets of mesh sizes 19.5, 22.5, 26.0, 29.0, 31.5, 35.0, 39.0 and 45.0 mm between adjacent knots. The nets were 25 m in length and 1.5 m deep. They were set in the littoral zone between 20:00 and 08:00 hours. The minimum effort was 4 series.

The efficiency of this series varies with the fish length (Jensen 1988). Jensen (1986, 1990) presents methods by which both the length distribution and the total, corrected number of fish (N_c) taken by any combinations of mesh sizes can be compared. The comparison is connected to a chosen level of efficiency (Jensen 1990). The maximum pooled relative efficiency of the used series towards Nesjø Arctic char was 3.00 for fish length 28 cm. This level was used for both materials, comparing the catches of salmonids >15 cm.

The fish length was measured to the fork and round weight was recorded. The age was read and growth in length back-calculated from scale impressions. The age of char was also found from otoliths. The condition factor (K) was calculated from fish length in cm (L) and round wet weight in g (W):

$$K=100WL^{-3}$$

Proportions of the different components of stomach contents were estimated as per cent volume for each stomach, and the mean per cent volume was calculated for the sample.

Results

Hydrography

The original Gåstjern was a small, thermally stratified lake. A temperature of 18.6°C was re-

Table 2. Temperatures (°C) in Gåstjern and the main basin of Finnkojsjø reservoir.

Depth m	Gåstjern		Main reservoir					
	23 Jun 1969	13 Jul 1971	27 Jun 1977	1 Sep 1977	25 Jun 1979	29 Jul 1979	29 Aug 1979	19 Sep 1979
0	18.6	11.1						
1	18.4	11.1	6.8	10.2	11.0	11.3	9.8	5.1
3	17.5	11.1	6.8	10.2	11.0	11.0	9.8	5.1
4	13.0							
5	11.0	11.1	6.8	10.2	11.0	10.7	9.8	5.1
7	10.0	11.1	6.8	10.2	11.0	10.2	9.8	
8								5.1
9	9.5							
10		11.0						

corded in its epilimnion in late June 1969 (Table 2). The maximum temperature recorded in the new, polymictic reservoir was 13.0°C on 12 July 1978. Generally the temperature has been 10–11°C in July–August. Cooling starts in September and 4°C should usually be reached by the end of the month. Ice break-up is in mid June and ice reforms in October.

A specific conductivity of 2.28 mSm^{-1} (at 25°C) was measured in Gåstjern in June 1969. Later records on 12 occasions in the ice-free periods have varied between 1.82 and 2.45 mSm^{-1}. Correspondingly, the pH of the surface water in Gåstjern was 7.1 and has since been in the range 6.7–7.3. The polymictic nature of the reservoir is reflected by these parameters. No vertical differences existed in pH and only very minor ones in conductivity.

The maximum winter temperature recorded was 1.5°C at 4 m depth in February 1974. On 14 April 1975 at 1 m depth, the conductivity was 9.60 mSm^{-1} and the pH was 6.1, a situation related to zero oxygen. Otherwise, in the periods of ice-cover, pH and conductivity were within the ranges 6.2–6.9 and 1.91–5.04 mSm^{-1}.

A smell of H_2S from the water leaving Finnkojsjø was first noticed in February 1973. Oxygen deficit in winter was recorded from 1973 to 1979 (Table 3), and was most distinct in the main reservoir. In the winters of 1975 to 1979, the smell of H_2S could be very intense.

The Secchi depth in Gåstjern was 6.9 m in 1969, and the Secchi colour was yellowish-green. Secchi depth decreased to 4.7 m in July 1971, 2.8 m in July 1979 and 2.5 m in September 1979, with a more distinct green colour. There was a mass occurrence of *Dinobryon bavaricum* Imhof all summer in 1979.

Table 3. Percentage of oxygen saturation in Gåstjern and the main basin of Finnkojsjø reservoir during ice-covered periods.

Depth m	Gåstjern			Main reservoir				
	7 Mar 1976	3 May 1977	2 May 1979	7 Mar 1973	5 Feb 1975	18 Apr 1975	7 Mar 1976	9 May 1978
1	70	68	84	67	61	1	64	60
2					38		64	
3				63				25
4		4	15					
6	37							

Table 4. The crustacean plankton of Finnkojsjø reservoir in 1979: number per m^3.

		Main reservoir				Gåstjern			
		25 Jun	29 Jul	29 Aug	19 Sep	25 Jun	29 Jul	29 Aug	19 Sep
Cladocera									
Holopedium gibberum		3,690	14	4	16	2,480	5		5
Daphnia longispina		11	3	1		70	10		
Daphnia galeata		7	90	120	190	1,900	3,940	1,260	270
Bosmina longispina		17	110	80	30	13	15	2	14
Bythotrephes longimanus		5	9	3	1		4	1	
Copepoda									
Diaptomus	N	11,380	10			6,380	18		
	C1	450	110			250	70		
	C2	23	680			15	500		
	C3		1,680	1			1,300	1	
	C4		2,340	21			1,540	18	
	C5		4,000	161			1,410	180	17
Mixodiaptomus laciniatus ♂			730	700	660		80	140	100
Mixodiaptomus laciniatus ♀			830	990	650		80	370	160
Mixodiaptomus laciniatus ♀/eggs			50	410	290			90	110
Acanthodiaptomus denticornis ♂			50	150	50		1	70	30
Acanthodiaptomus denticornis ♀			90	890	620		19	710	820
Acanthodiaptomus denticornis ♀/eggs				7	10			2	1
Heterocope saliens	C1	210				60			
	C2	110				17	2		
	C3	23							
	C4		1						2
	C5		30	1			18		3
	♂		70	30			40	60	4
	♀		130	30	3		70	60	21
Cyclops scutifer	N	180	5,620	1,010	110	350	16,710	1,480	90
	C1		24	1,370	1,560		100	1,980	680
	C2		5	2,330	790		1	4,340	1,740
	C3			1,480	4,070			2,820	5,700
	C4			1	40				180
	C5	24				40			
	♂	90	10			1,200	5		
	♀	220	70	50	2	710	200	28	
	♀/eggs	210	70	6	2	510	210	1	
Megacyclops gigas	N	540	1			1,040	1		
	C1	410				335			
	C2	50				7			
	C3	1							
	C4								
	C5			1					
	♂			1	1				
	♀				2				6

Crustacean plankton

The seasonal cycles of the various species are shown by the 1979 material (Table 4). Small *Holopedium gibberum* Zaddach occurred in relatively large numbers in June, but the species had almost disappeared in late July. *Daphnia galeata* Sars showed a regular cycle in Gåstjern with a peak of about 4,000 m^{-3} in July. Its numbers in the main reservoir were small, but increased

Table 5. The crustacean plankton of Finnkojsjø reservoir in 1971–77, number per m^3.

	Main res. 14 Jul 1971	Gåstjern 27 Sep 1973	Main res. 27 Jun 1977	Gåstjern 29 Jun 1977	Main res. 1 Sep 1977
Cladocera					
Holopedium gibberum	2,610		3,780	2,100	
Daphnia longispina	11,900		3	1,230	19
Daphnia galeata		750	3	630	2,330
Bosmina longispina	1,340	70	1		
Bythotrephes longimanus	26				
Diaphanosoma brachyurum					19
Copepoda					
Diaptomidae N + C	690		3,740	300	300
Mixodiaptomus laciniatus ad.					190
Acanthodiaptomus denticornis ad.		1,090			3,080
Heterocope saliens	1,920				
Cyclops scutifer	2,250	120	160	6,600	3,560
Megacyclops gigas	990		2,030	230	

throughout the summer. Three other cladocerans, *Daphnia longispina* O.F.M., *Bosmina longispina* Leydig and *Bythotrephes longimanus* Leydig occurred in small numbers in both basins.

Two species of Diaptomidae were present. Nauplii and copepodites were not distinguished at the species level. Nauplii were at their peak in June. In late July, the majority had grown to copepodite stages 3–5. *Mixodiaptomus laciniatus* (Lillj.) reached the adult stages in late July. Egg-carrying females were at their peak in late August, but many were also present in mid September. In contrast, the cycle of *Acanthodiaptomus denticornis* (Wierz.) was one month later. This species produced eggs only after 20 September. *Heterocope saliens* (Lillj.) occurred in small numbers. Its cycle was similar to the diaptomids, but the adult maximum occurred in July. Two distinctly separate generations of *Cyclops scutifer* Sars were present all summer. Survivors from the previous year occurred as adults in late June. Their numbers decreased, but egg production took place throughout the summer. Nauplii of the second generation were subsequently produced and had their maximum in July. In mid September the majority had reached copepodite stage 3. *Megacyclops gigas* (Claus) were present as nauplii and small copepodites in late June. They then disappeared from the open water. A few adults occurred in late August–September.

The crustacean communities in Gåstjern and the main reservoir were quite different. Gåstjern had larger numbers of *D. galeata* and *C. scutifer*, but the differences became less distinct during the summer. Except for the occurrence of *H. gibberum* in June, the community of the main reservoir was almost completely composed of copepods. The numbers of diaptomids were double those in Gåstjern. This seems related to *M. laciniatus*, as *A. denticornis* occurred in about equal numbers in the two basins.

The situation was quite different in July 1971 (Table 5), when cladocerans, especially *D. longispina*, dominated the main reservoir. The number of diaptomids was low. In September 1973, *A. denticornis* was the only diaptomid in Gåstjern. *D. longispina* was more abundant than *D. galeata* in Gåstjern in June 1977. In September 1977 the number of *D. galeata* in the main reservoir was 2,300 m^{-3} compared with 190 m^{-3} in September 1979. A few *Diaphanosoma brachyurum* were also recorded in the main reservoir. Otherwise, the pattern known from 1979 was already established.

The most distinct long-term changes were the decline of *D. longispina* and *B. longispina*, and

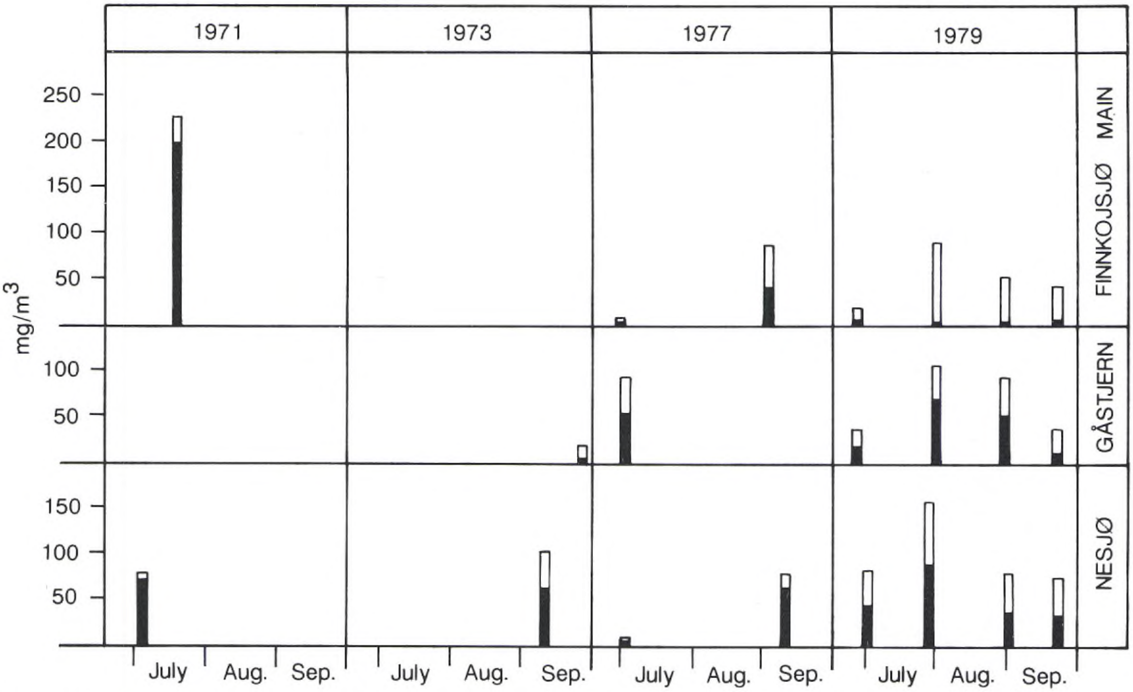

Fig. 4. Biomass (mg m^{-3} dry weight) of plankton cladocerans (black columns) and copepods (open columns) in Gåstjern, the main basin of Finnkojsjø, and in the Nesjø reservoir.

the expansion of the *D. galeata* and copepod populations.

The crustacean biomass in the main reservoir in July 1971 was 231 mg m^{-3} (dry weight), cladocerans representing 86 % (Fig. 4). In 1979, it reached 93 mg m^{-3} in July, copepods making up 97 % of the biomass. The biomass was somewhat higher in Gåstjern that year, and was dominated by *D. galeata*. In both cases the biomass was smaller for most of the 1979 season than in Nesjø, where the cladocerans were heavily predated by Arctic char.

Macrobenthos

The original Gåstjern apparently had a low level of macrobenthos, dominated by Chironomidae (Table 6). The abundance of *Gammarus lacustris* Sars was definitely underestimated. When sampling took place, it was swarming in open water and at the surface, eating *Picea abies* (L.) pollen. The numbers and biomass of Chironomidae increased significantly in 1971, after the first flooding. The biomass of total macrobenthos was more than doubled since 1969.

Table 6. Macrobenthos in Gåstjern as mean of the depth zone 1–7 m, wet weight per m^2 (g).

	24 Jun 1969	14 Jul 1971
Oligochaeta	0.397	0.773
Gammarus lacustris	0.254	0.020
Ephemeroptera	0.003	
Trichoptera	0.074	
Chironomidae	1.444	5.693
Other insects	0.006	0.002
Pisidium	0.722	1.392
Sum	2.927	7.880

Fish

The year before flooding took place, Gåstjern had small populations of brown trout and Arctic

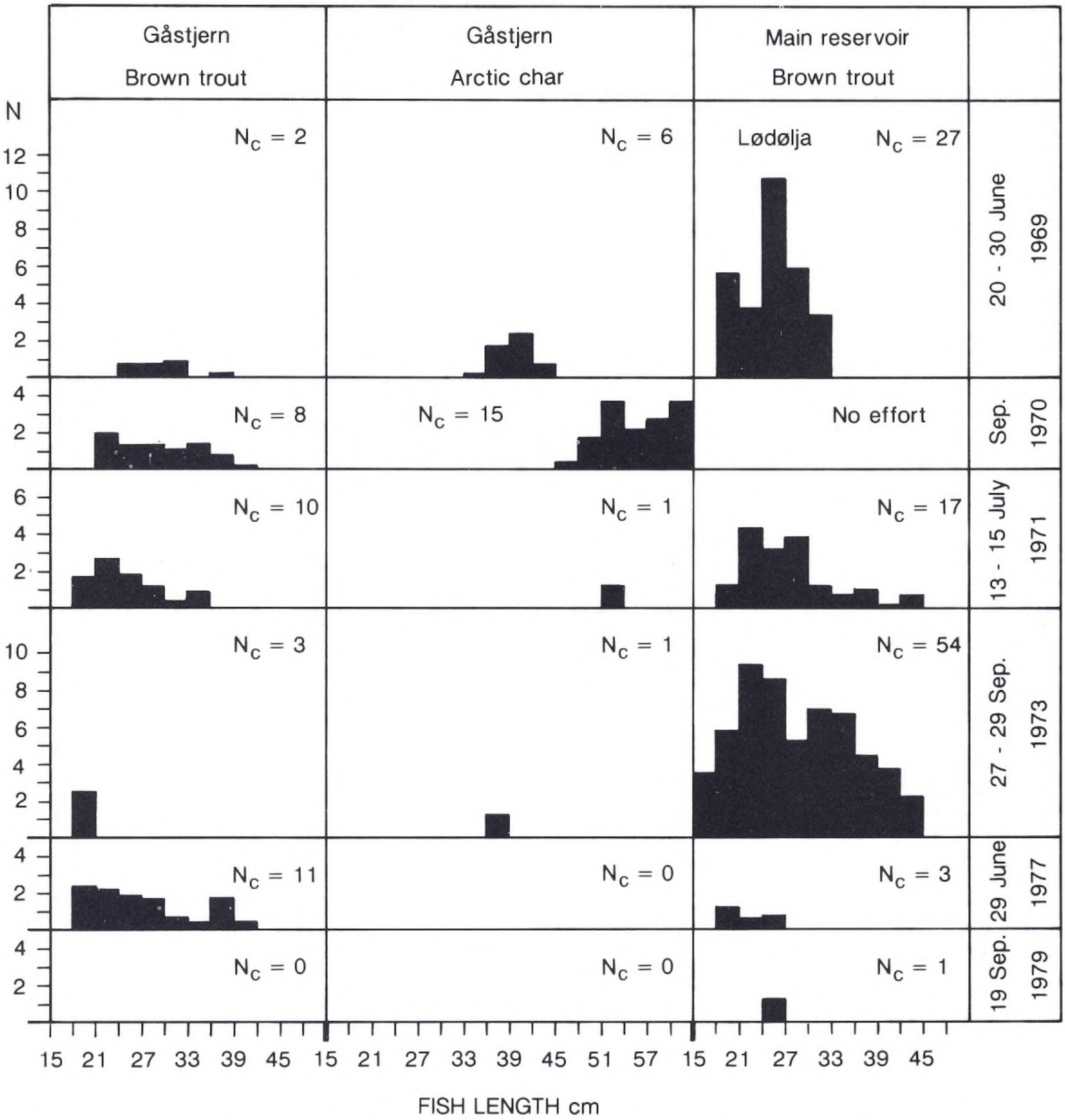

Fig. 5. Number of fish caught per series of nets and corrected for net efficiency relative to fish length (N_c), pooled in 3 cm length classes.

char (Fig. 5). The trout were 24–33 cm long. The char were larger and their mean condition factor was 1.70. The river Lødølja was more densly populated with brown trout. The smallest caught were 18 cm.

More and larger fish were taken in Gåstjern in autumn 1970 compared with 1969. The char catch was quite extraordinary. It comprised 11 char of length 46.5–60.0 cm, weight 1.7–3.8 kg and a mean condition factor of 1.72.

The last char was taken in Gåstjern in September 1973. The trout catch was then at its maximum with a N_c of 54. In 1977, their number had declined, and most were taken in Gåstjern. In

Table 7. The maximum annual length increase in cm of brown trout taken in the original water system and in Finnkojsjø reservoir during 1971–77.

		Year of life						
		1	2	3	4	5	6	7
Lødølja river	1969	6.5	5.5	6.0	6.0	6.5	4.5	3.5
Gåstjern	1969	6.5	6.0	7.5	8.5	12.0	11.0	8.0
Finnkojsjø	1971	7.5	9.0	12.0	13.0	12.0	12.5	11.0
Finnkojsjø	1973	8.0	11.5	12.5	11.0	11.5	8.5	3.0
Finnkojsjø	1977	5.5	11.0	11.0	11.5	11.0	8.0	3.5

1979, probably no fish had survived the previous winter. Only two trout were taken near the outlet of Lødølja.

The mean length of all age classes of trout increased after impoundment. These figures do not express the growth potential of the reservoir, as only some trout stayed there for the entire growing season. The potential growth is better documented by the maximum growth (Table 7). The mean growth of the Lødølja trout was about 4 cm a year during the first four years of life, with a maximum of about 6 cm. The older trout grew less. The trout grew significantly better in Gåstjern. Compared with the river population, the maximum growth of year classes 3–5 was doubled in 1971. Also age classes 6 and 7 had a maximum growth of 11.0–12.5 cm a year. In 1973 and 1977, the growth of these age classes had decreased.

The mean length of 8 char aged 7 taken in Gåstjern in 1969 was 40.0 cm. They had grown about 5 cm a year during their first 3 years, later about 7 cm a year.

The mean condition factor of the trout living in the original water bodies was about 1.10. After impoundment it increased to 1.20. The Arctic char were exceptionally fat as mentioned above, with a maximum individual condition factor of 2.19 in 1970.

The Gåstjern trout were mainly feeding on *G. lacustris* in June 1969 (Fig. 6). The stomach contents of the char were composed of 71 % *G. lacustris* and 29 % *Daphnia*. In July 1971, Gåstjern trout had mainly eaten Trichoptera and Chironomidae. Trout in the main reservoir had taken 62 % Chironomidae. In both cases about 10 % crustacean plankton was *B. longimanus*. In late September 1973, *G. lacustris* made up 45 % of the stomach contents of all trout caught in the main reservoir, but only 0.5 % of the trout caught near the outlet of Lødølja. A few *G. lacustris* were still eaten in June 1977, but the main food was Chironomidae.

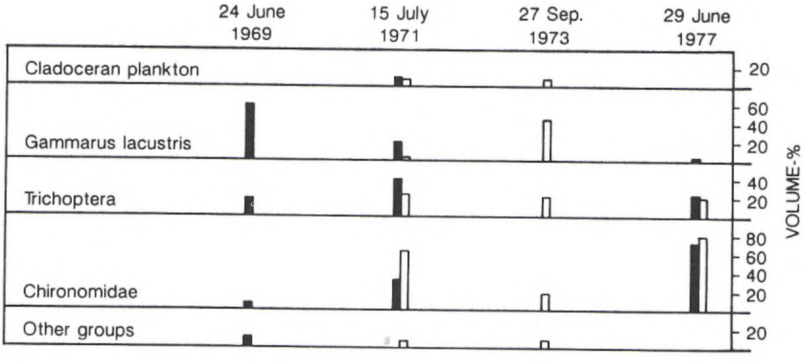

Fig. 6. Stomach contents of brown trout in Gåstjern (black columns) and the main part of Finnkojsjø reservoir (open columns) as mean per cent volume.

Discussion

The Finnkojsjø reservoir has the soft water characteristic typical of waters in many parts of Scandinavia. Its surface water was neutral, and no indices of acid precipitation existed. On 18 April 1975, complete oxygen depletion existed in the main reservoir. Based on reports on the smell of H_2S, this has probably been the situation in all winters since, allthough 1978 was an exception. This winter the water was left 5 m above the lowest permitted level. The oxygen saturation was 60 % at 1 m and 25 % at 3 m depth on 9 May. A similar situation existed in the Gåstjern basin in the winters of 1976–79. The oxygen depletion was caused by the decomposition of the flooded vegetation and the reduction processes taking place in humic water. The water volume left in Finnkojsjø at its lowest level is too small to withstand these processes. Oxygen deficiency is not unusual in eutrophic lakes and reservoirs (Wetzel 1975, Frost et al. 1978), but has not been reported from boreal, oligotrophic reservoirs.

The temperature in Finnkojsjø is excellent for the growth of brown trout, which minimum temperature is about 4°C (Elliott 1975). Thus, the usual growing season is about 105 days, from 15 June to 30 September, the same as in Nesjø. For most of the growing season the temperature is just below the optimum of 13°C found by Elliott (1975).

The crustacean plankton biomass reached 231 mg m^{-3} in July 1971, cladocerans representing 86 %. This was comparable with the 219 mg m^{-3}, 98 % of which were cladocerans, recorded in Nesjø in July 1970. The continuously reproducing cladocerans took advantage of a potential fertilizing effect and the large amounts of debris from the flooded ground. The univoltine copepods needed 2–3 years to reach numbers corresponding to the carrying limits of the reservoirs.

In 1979, the biomass was about half the 1971 level. In Gåstjern the proportion of cladocerans to copepods was similar to that in Nesjø. The biomass was smaller than in Nesjø, despite the heavy predation on Nesjø cladocerans by Arctic char. On the other hand, both the weight of char caught per series of nets and the size and biomass of cladocerans in Nesjø were larger than in other lakes (Jensen 1988). Thus, the interactions between them were very successful, probably close to an optimal situation. The crustacean community of the Finnkojsjø main reservoir was quite extraordinary, being dominated by diaptomids, which at their maximum comprised 97 % of the biomass. *H. gibberum* was the only cladoceran of any noticeable density, but this population collapsed before the end of July. The copepods seemed to tolerate the winter oxygen depletion better than the cladocerans. They can survive such conditions in the form of resting eggs and also, in the case of *C. scutifer*, as diapausing copepodites (Elgmork and Nilssen 1978, Elgmork et al. 1978). Without competition from cladocerans, the herbivore *M. laciniatus* and *A. denticornis* in the main basin established a biomass just below the level of all the crustaceans in Gåstjern. The most usual diaptomid in these areas and the dominating one in Essand-Nesjø, *Arctodiaptomus laticeps* (Sars), was never found in Finnkojsjø.

The biomass of Chironomidae and the total macrobenthos increased in Gåstjern after impoundment, a situation known from the Gautsjøen reservoir (Jensen 1982). This is confirmed by the stomach contents of the fish. As in Nesjø the stomachs were full of Chironomidae in the beginning of the growing season. A high production of Chironomidae is a general tendency in impoundments all over the world (Jensen 1988). It is probably connected with certain species that are able to tolerate water level fluctuations and live on the terrestrial plant material stored in the reservoirs. In Finnkojsjø, as in other Scandinavian mountain reservoirs, that means large deposits of peat, still present 60–70 years after impoundment and lasting for 100 years or more. In windy weather, waves erode peat fragments and they are sedimented all over the reservoir bottom.

In Finnkojsjø *Gammarus lacustris* tolerated the water level fluctuations quite well. By 1973, it had spread from Gåstjern and had become the primary food also for fish in the main reservoir. It was still present in June 1977. This species disappears or loses its importance as fish food when water level fluctuation exceeds 5 m (Aass 1969). It did not, for example, occur in the stomachs of fish taken in Essand, regulated 6.6 m, 3 years after impoundment (Jensen 1988).

Arctic char generally outnumbers brown trout in Scandinavian reservoirs (Jensen 1979, Aass 1984, Aass and Borgstrøm 1987). In Finnkojsjø it died out before the trout. The last one was caught in 1973. This coincided with the more extensive draining of the reservoir, which indicates that Arctic char could be less tolerant to a low oxygen level than brown trout. However, the smallest char taken before impoundment was 34.0 cm and 635 g. Apparently, a reproduction problem already existed in the original Gåstjern. Newly flooded ground of this type offers no spawning facilities. In Nesjø the char succeeded by establishing a migration pattern between the foraging areas in the newly inundated regions and the spawning grounds in Essand (Jensen 1988).

A brown trout population developed in Finnkojsjø, mainly based on the stock of the former river. The catch per effort was 2.2 kg per net as the mean of mesh sizes 39.0–26.0 mm in September 1973. This equals the catches obtained in other impoundments during the first 2–3 years (Jensen 1979, 1988, Bergan 1985, Koksvik 1985). About 30 % of the trout taken in 1973 were larger than the maximum length of the original river stock. The fraction of the population <20 cm showed that recruitment took place. All indications for satisfactory trout fishing were present. The trout were decreasing in 1977, most having survived in Gåstjern. Two years later the population had died out. Only two were taken close to the outlet of Lødølja. The collapse of the trout population is connected with the oxygen depletion. The possibility of surviving in the Gåstjern basin existed, but those which survived were able to spread all over the reservoir during summer.

After flooding, the annual growth of the trout increased from an ordinary level to 10 cm and their condition factor to 1.20. This equals the growth recorded in other Norwegian impoundments (Bergan 1985, Koksvik 1985, Jensen 1988). The growth in length of the Gåstjern char was above average. Their condition factor was exceptionally high, and equivalents have not been found in the literature. This was a result of few char and large numbers of *Gammarus* and *Daphnia*. The only feature distinguishing Gåstjern from other small lakes in these mountains, is the large quantities of *Picea abies* pollen deposited there, due to a dominant wind direction and special topographical conditions. This may have direct and indirect positive effects on the invertebrate production. Pollen was found in *Gammarus* intestines.

The food of salmonids in Scandinavian reservoirs has mainly been Entomostraca and terrestrial insects (Dahl 1932, Nilsson 1961, 1964, Aass 1969). In Finnkojsjø, Chironomidae were the primary or a very important prey, as they were in Nesjø (Jensen 1988) and in reservoirs in the U.S.S.R. (Miroshnichenko 1979), Czechoslovakia (Losos 1976, 1977), England (Crisp et al. 1978, Moore 1982), Ohio (Paxton et al. 1981) and California (Marrin et al. 1984).

The invertebrate diversity in reservoirs is low, as most littoral species can not tolerate the water level fluctuations. Thus, food supply is often insufficient and consequently fish growth is poor. Ten years after Nesjø was made, its estimated yield was 5 kg ha^{-1} of Arctic char weighing 300–500 g. The potential yield was expected to be 8 kg ha^{-1} (Jensen 1988). This production was based on Chironomidae, *Daphnia* and terrestrial insects. Finnkojsjø had similar or better possibilities for supporting brown trout; Chironomidae, *Gammarus*, *Daphnia*, *Bythotrephes* and terrestrial insects.

The Granasjø reservoir is located 650 m a.s.l. in the same county as Finnkojsjø. It was made in 1980, mainly on bogs and wetland. At its lowest water level, it covers 0.49 km^2 with a maximum depth of 3.6 m and a mean depth of 2.0 m. The renewal time of its water in winter is about half that of Finnkojsjø. A large and flourishing population of brown trout has existed in Granasjø ever since the reservoir was made.

The regulation of Finnkojsjø should be changed. Increasing the minimum depth by 2 m and the corresponding volume to $3 \cdot 10^6$ m^3 would probably ensure acceptable oxygen levels. The oxygen lode at the beginning of the minimum water period would increase by a factor of 2.6 or more, and the amount of oxygen supplied during the period does not change. The fish would survive and the crustacean plankton change in favour of cladocerans. Positive effects on the production of *Gammarus* and Chironomidae should be expected.

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Influence of Water Flow, Water Temperature and Light on Fish Migration in Rivers

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Abstract

Water flow, water temperature and light are environmental variables that influence when fish migrate and the intensity of the migration itself. These variables apply both to up- and downstream migration, but their effects may vary among rivers and species. During the ontogeny, migratory fish in different life history stages are transported downstream by the water flow. Changes in water flow may influence when the fish migrate, migratory speed and the direction of migration. To be carried downstream, the fish, however, must position themselves within the water column and actively swim out of sloughs and backwaters. High water discharge may stimulate the river ascent. Large Atlantic salmon, for instance, depend on a certain amount of water to ascend a river. Furthermore, high flow may aid the fish in finding the mouth of the stream they are going to enter. To much water, however, may temporarily stop the river ascent. Water temperature is an important factor initiating up- and downstream migrations of several fish species. In particular, this may be the case in rivers where freshets do not regularily occur at the time when the environmental shift is favourable. Migrations of juveniles and adults are mainly nocturnal, but sometimes diurnal. When the migration occurs during dark hours this is expected to be an adaptation to avoid visual predators.

Introduction

Water flow, water temperature and light are environmental variables that influence both when the fish migrate, and the intensity of migration (Northcote 1984). These factors apply both to up- and downstream migration. Very often, the migration is connected to the transition between life history stages, e.g. between hatching and the start of exogenous feeding of river spawning whitefish, when juvenile salmonids smolt from freshwater parr to juvenile fish that will feed in the ocean, and when eels transform from immature yellow eels in freshwater to maturing silver eels that are going to spawn in the ocean. In such cases, factors influencing the timing of the transition may also influence the timing of the migration itself.

The ultimate causes of the migration is probably to increase the product of survival and growth to maximize Darwinean fitness over the entire life cycle (Gross 1987). In cases when a single habitat provide insufficient resources for the entire life cycle, fitness is increased by moving between different habitats supporting variable needs during the ontogeny.

Typically, increasing and decreasing photoperiod is the predictive, proximate factor indicating to the fish the season of migration (Eriksson et al. 1982). The photoperiod indicates the season to the fish, as the day length is the same on each specific day every year. Annual variation in time of migration, however, cannot be induced by photoperiod, but by water flow and water temperature. The latter two are anticipating factors stimulating migration depending on local conditions. During recent years a growing body of literature has demonstrated how water flow and water temperature regulate fish migrations. Even though there has been earlier reviews on this subject (e.g. Banks 1969, Northcote 1984, Smith 1985), I feel that due to many new results, especially from the Norwegian River Imsa, it is now justified to review the literature. I have put emphasis on presenting new results, not reviewed in earlier works. Many of the recent studies have given quantitative models predicting start and speed on migration based on water flow and water temperature, and qualitative relationships between migration and light intensity (e.g. Hvidsten 1985, Jonsson and Ruud-Hansen 1985, Næsje et al. 1986, Vøllestad et al. 1986, Jensen et al. 1989). Older studies are, however, included to complete the presentation. In this paper I discuss the influence of water flow, water temperature and light on up- and downstream migration of fish in rivers. I treat each factor separately, but in some cases this has been difficult since different factors may trigger the same behaviour in different rivers. This review is chiefly focused on studies of diadromous fishes.

Water flow

Downstream migration

Water flow in rivers provides the downstream displacement of all life history stages of migratory fishes. Eggs of many species are passively transported downstream by the water flow to lakes or estuaries with better rearing conditions for the young, e.g. the shad (*Hilsa ilisha*), striped bass (*Morone saxatilis*), mountain mullet (*Agonostomus menticola*), blueback herring (*Alosa aestivalis*) and rainbow smelt (*Osmerus mordax*) (Talbot 1966, Ganapti 1973, Gilbert and Kelso 1971, Loftus et al. 1984, Johnston and Cheverie 1988). In riverine species with adhesive eggs (e.g. osmerids, cyprinids, coregonids), the larvae are transported downstream by the water flow. In river spawning coregonids, the eggs stick to the stony substrate, but mechanical agitation due to increased water flow during the spring freshet, influence the hatching time of eggs (Næsje et al. 1986). The migration from the river to the lake where the larvae start exogeneous feeding commences almost immediately after hatching (Lindroth 1957). Næsje et al. (1986) observed that the outdrift of newly hatched cisco (*Coregonus albula*) and whitefish (*Coregonus lavaretus*) larvae in a Norwegian river started concurrently with the spring flood, and the maximum number of drifting larvae per unit of time were significantly correlated with the daily rate of increase in water discharge. The effect on the eggs by the agitation due to increased flow was demonstrated in laboratory (Næsje and Jonsson 1988) and field (Næsje et al. MS) experiments. In the laboratory experiment, eyed eggs were divided into four main groups: two were incubated at river temperature (2–10°C) and two in heated water (6.5–8.5°C). At both temperatures, eggs kept in motion by flowing water hatched earlier (heated water: 380 ± 6.4, natural water: 417 ± 6.6 degree-days from fertilization to 50 % hatching) than those laying undisturbed (heated water: 513 ± 10.5, natural water: 470 ± 7.3 degree-days). Furthermore, eggs agitated during incubation hatched with greater synchrony than those incubated undisturbed. The increased water flow in the Gudbrandsdalslågen river synchronized the hatching of the coregonid eggs and transported the newly hatched larvae downstream the river. In a recent field experiment (Næsje et al. MS) artificial freshets were created in the river before the natural spring flood. Immediately after the early flooding started, drifting larvae appeared in the river.

High water discharge in rivers also provides downstream movement of juveniles of a variety of fish species (Applegate and Brynildson 1952, Northcote 1962, 1969, Potter 1970, Priegel 1970, Gale and Mohr jr 1978, Ewing et al. 1980, Sjöberg 1980, Arawomo 1981, Hartman et al. 1982, Youngson et al. 1983, Corbett and Powles 1986, Bilby and Bisson 1987, Jonsson et al. 1988, 1989). For instance, the movement of recently transformed sea lamprey (*Petromyzon marinus*) occurs on the rise and crest of floods resulting from the general spring ice-break-up in late March or early April in the River Carp Lake, Michigan (Appelgate and Brynildson 1952). A similar relationship between downstream movement and spring flood was demonstrated for fry of coho salmon (*Oncorhynchus kisutch*) over a 10-year period in Carnation Creek, British Columbia (Hartman et al. 1982). The time period over which downstream movement took place varied widely between years. During seaward movement daily numbers fluctuated widely. Peaks of movement coincided with or appeared slightly before freshet peaks. Hartman et al. (1982) compared the number of fry moving seaward during the night closest to the peak flow period, or during the night before, with the number moving on the three previous nights. In 94 of 122 cases (77 %) the number of fry moving during the night of peak discharge, or during the night before, was significantly higher than in any of the three preceding nights. Stream temperature is apparently without effect on the release of potentially emigrant coho fry from this stream.

The downstream migration of salmonid smolts may also in some rivers be initiated by increased water flow (Berry 1932, 1933, Allen 1944, Österdahl 1969, Hesthagen and Garnås 1986). Hesthagen and Garnås (1986) studied the downstream migration of Atlantic salmon (*Salmo salar*) smolts during May and June in River Orkla, Norway. River Orkla has quite low water temperatures in summer (average 113 days with water temperatures over 6.5°C), and high fluctuations in water discharges (average yearly water discharge 30 m^3s^{-1}, but it sometimes exceeds 1,000 m^3s^{-1} during floods). Hesthagen and Garnås (1986) found that the smolt migration was initiated by the first spring peak in water discharge (>100 m^3s^{-1}), when the temperature was 2–3°C. Furthermore, significantly more smolts migrated when the discharge was increasing, followed by a drop in water temperature, than under the opposite conditions.

In catadromous eels, several authors maintain that the water flow is a major factor regulating the time of the seaward migration of adult eels (e.g. Lowe 1952, Jens 1952/53, Deelder 1954, 1984, Frost 1950, Burnet 1969, Hain 1975, Todd 1981, Vøllestad et al. 1986, Bergersen and Klemetsen 1988). For instance, Frost (1950), Lowe (1952) and Jens (1952/53) found that catches of European silver eels in rivers increased with a rise in water level. Moreover, Tesch (1977) maintained that increased water discharge encouraged the eels to migrate. Deelder (1954) found that in the Dutch Polders, which are usually kept at a constant water level, silver eel catches varied in relation to the discharge which was controlled by sluices. Vøllestad et al. (1986) found that the run of European silver eels (*Anguilla anguilla*) in River Imsa, Norway, started earlier in autumns with high water discharge, than in autumn with low flow. Mean water discharge during August–October explained 65 % of the total variation in the start of the run.

The water flow in rivers also appears to influence the direction of migration (Lowe 1952, Deelder 1954, Fried et al. 1978). Deelder (1954) studied the migration of silver eels in a Dutch canal in which the water moved in alternate direction at low speeds and with fish traps on both sides. In this system the direction of the migration was influenced by the direction of the water flow in the canal. The silver eels migrate with the water flow. The importence of the water current for the downstream navigation is also indicated by observations of Atlantic salmon in lakes. Fried et al. (1978) observed that water current was the main factor influencing the route of seaward migrating Atlantic salmon smolts. The smolts usually moved in the same direction as current flow during ebb and flood tides. Similarly, Allen (1944) and Mills (1964) reported the passages of smolts through lakes were slower than those through rivers. Furthermore, Thorpe et al. (1981) tracked Atlantic salmon smolts through Loch Voil, Scotland. They found that the direction of displacement of smolts and movement of water at a depth of 1 m was positively correlated ($P<0.001$). Release experiments of smolts in River Imsa and in two lakes, 3 and 11 km upstream the river, show that the migration was delayed when the fish was released in or above the lakes (Hansen et al. 1984). Low water velocities in lakes may also explain why salmon stocked in lakes descend the watercourse outside the normal smolting period, or do not leave the lakes at all (Munro 1965, Frantsi et al. 1972, Hansen 1987), although it may be uncertain to compare hatchery with wild salmon. On the other hand, the dependence of the migrating fish on water current may differ among populations and species. Parr of Atlantic salmon reared in Newfoundland lakes had apparently no problems in finding their way out of the lakes and downstream (Hutchings 1986). In another species like sockeye salmon (*Oncorhynchus nerka*), where the juveniles naturally rear in lakes before smolting and migrating to sea, low current velocities obviously are no hinderance for a successful seaward migration. This fish seem to be genetically adapted to slow flowing systems, and have an innate behavioural program helping them finding the outlet (Groot 1965). A similar genetic program may also help rainbow trout (*Oncorhynchus mykiss*) fry orient in complex river systems (Kelso and Northcote 1981). Thus, populations adapted to systems with low flow may have evolved navigation systems that are independent of the direction of the water flow.

Water flow may also determine the speed of descending fish. Raymond (1968) compared the migration rate of yearling chinook salmon (*Oncorhynchus tshawytscha*) in Snake and Columbia Rivers during periods of low (Columbia river: 4,248 m^3s^{-1}, Snake river: 1,416 m^3s^{-1}) and moderate (Columbia river: 8,495 m^3s^{-1}, Snake river: 2,265 m^3s^{-1}) water discharges. The rate of migration was directly related to water flow: it was 21 km day^{-1} at low and 37 km day^{-1} during moderate river discharges. Vøllestad et al. (1986) studied the downstream migration of European silver eels during August to December in River Imsa, Norway. They found that the downstream migration of silver eels occurred earlier in years with high than with low water discharge. Based on this and a series of field experiments, they concluded that high water discharge increased migration speed. The downstream migration speed of transplanted silver eels was correlated with water discharge and water temperature. Variation in water discharge alone explained 85 % of the total variation in migration speed.

Downstream migration during high water flow appears favourable for several reasons. Firstly, the fish are transported downstream without expending much energy in active swimming. They must, however, actively stay in the current and move out of sloughs and backwaters (Hansen and Jonsson 1985). Secondly, high flow may provide shelter to the migrating fish (Hvidsten and Hansen 1989). At high discharges, river water may be turbid and often the water surface form ripples. Thirdly, high water flow appears to influence the timing of the seaward migration (Jonsson and Ruud-Hansen 1985). Forthly, the water current determine the speed and the direction of the migration (Thorpe et al. 1981). When the current velocity is low as in lakes, the fish may be delayed and have difficulties in finding their way downstream.

Upstream migration

Water flow appears to be an important factor stimulating upstream migration of various fish species, especially in rivers with highly fluctuating water levels during the migration periods (e.g. Huntsman 1948, Hayes 1953, Stuart 1953, 1957, Saunders 1960, Harriman 1961, Banks 1969, Alabaster 1970, Asplund and Södergren 1975, Libosvàrsky 1976, Sjöberg 1980, MacCrimmon and Gordon 1981, Jellyman and Ryan 1983, Holtby et al. 1984, Potter 1988, van den Berghe and Gross 1989, Webb and Hawkins 1989, Jonsson et al. 1990). Fluctuating water levels may, however, have more pronounced effects in small than in large rivers.

Jellyman and Ryan (1983) showed that the largest upstream migrations of elvers of *Anguilla australis* and *A. diefenbachii* in Lake Pounui, New Zealand, coincided with the greatest seasonal rainfall and the smallest migrations with the least rainfall. They found a relationship between the total number of elvers per season and the total rainfall, so that low rainfall during the main migratory period (November–April) resulted in a small seasonal migration, and vice versa.

In the Norwegian River Imsa, a small river with high water flow during autumn, the number of ascending adult Atlantic salmon increased with increasing water discharge (Jonsson et al. 1990). Furthermore, in Deer Creek Junior, Washington, the ascent of female coho salmon increased with raising stream level (van den Berghe and Gross 1989). Similarly, Saunders (1960) observed in Ellerslie Brook, Prince Edward Island, that adult Atlantic salmon entered the river during autumn freshets, and remained at the head of the estuary during periods of low flow. Potter (1988) tracked Atlantic salmon in the estuary of the River Fowey, south-west England. He observed that most fish entered freshwater during periods of increased freshwater discharge. Low river flow delayed the migration of salmon into the river, and many fish stayed for several weeks or even months in the estuary before entering fresh water. However, the fish did not always enter the river on the first increase in flow. One reason may be that they move quite large distances away from the river mouth and do not detect all floods. In River Narraguagus in Maine, a stream with very low summer levels and high rates of discharge during spring, the main ascent of salmon started during the first freshet after 15 May (Harriman 1961). However, the study of Hellawell et al. (1974) on upstream migration of salmonids in River Frome, England, a river with only minor seasonal water level fluctuations, showed that salmonids tended to move upstream at discharges lower than those generally available. This may be attributed to the equitable flow pattern of the English chalk streams. Similar results have been reported by others, e.g. for Atlantic salmon (Huntsman 1948, Hayes 1953) and pink salmon (*Oncorhynchus gorbuscha*) (Davidson et al. 1943).

High water discharge during the upstream spawning migration seems more essential for large than small salmon. For instance, in the Deer Creek Junior, the ascent of female coho salmon was significantly correlated with water level (van den Berghe and Gross 1989). Large females entered the creek at peak discharge and progressively smaller ones entered as waters receded, while no such trend was found among males. In the River Imsa the larger, multi-sea-winter salmon were more dependent on high water levels when migrating than the smaller one-sea-winter fish (Jonsson et al. 1990). The adult salmon stayed in the fiord area near the river mouth, but most of the multi-sea-winter fish did not ascend until the autumn increase in water discharge. In this river, low water discharge during summer seemed to delay upstream movement of large salmon more than small ones.

Upstream migration during high water flows appear disadvantageous for the fish, because of increased energetic costs relative to low flow situations. However, this increased cost is probably balanced by the increased protection offered by the increased flow.

Large rivers, with high water discharges, may aid the fish in finding the mouth of the stream they are going to enter (Malmqvist 1980, Jellyman and Ryan 1983). This is supported by the fact that the number of fish straying to other rivers seem to decrease with increasing river size (Hansen 1980, Berg and Jonsson 1989), and that salmon released directly in the sea as smolts, enter the largest among the nearby rivers when they return as adults (Hansen et al. 1989).

Very high water discharges, however, may temporarily stop upstream migration of some fish species (Davidson et al. 1943, Sörensen 1951, Stuart 1957, Malmqvist 1980, Jensen et al. 1989). The upstream migration of lamprey in Länsmansbäcken, a small stream in southern Sweden, ceased at times of heavy rainfall (Malmqvist 1980). In an experiment, Sörensen (1951) found that elvers of European eel stop their upstream migration at high flows. A flow rate of 0.6–0.9 ms^{-1} did not greatly impede the eels' upstream movement, whereas a rate of 1.5 ms^{-1} stopped all upstream movement of eels measuring less than 15 cm. In brown trout the upstream spawning migration may be delayed during periods of exceptionally high flow (Stuart 1957). In the Norwegian river Vefsna, a nine-year study has demonstrated that ascending Atlantic salmon is stopped by the first water fall if water discharge is above but not below 300 m^3s^{-1} (Jensen et al. 1989). This shows that water flow is important for the river ascent of migratory fish, either because a certain river discharge is needed for the fish to move upstream, or because they are unable to ascend before the discharge is below a threshold value.

Water temperature

Downstream migration

Water temperature is an other proximate factor initiating downstream fish migrations. This may especially be the case in rivers where freshets do not regularily occur simultaneously with the time of downstream movement.

Increasing water temperature in spring is important for the initiation of the smolt run of several salmonid species in many rivers (e.g. Foerster 1937, White 1939, Mills 1964, Hartman et al. 1967, Österdahl 1969, Bjornn 1971, Wagner

1974, Baglinière 1976, Fried 1977, Solomon 1978, Raymond 1979, Jonsson and Ruud-Hansen 1985, Holtby et al. 1989, Jonsson et al. 1989). White (1939), Mills (1964), Österdahl (1969) and Solomon (1978) have found that the downstream movements of smolts were closely correlated to rising water temperature. For Atlantic salmon and brown trout, they found that most smolts descended when the river temperature was above 10°C. Other authors are critical to defining a threshold temperature for the onset of the downstream smolt migration. For instance, in sockeye salmon and Atlantic salmon Foerster (1937) and Melnikova (1970) observed that the smolt run started earlier if the average water temperature were higher than normal in the preceding months. Furthermore, Jonsson and Ruud-Hansen (1985) studied the downstream migration of Atlantic salmon smolt during 8 years in the River Imsa, Norway. They correlated water temperature, water flow, cloudiness and lunar cycle with timing of the yearly descent of smolts, but only water temperature was significantly correlated with the time of smolt descent. The development in water temperature between 9 April and 16 May explained 91, 95 and 89 % of the yearly variation in date of 25, 50 and 75 % yearly cumulative smolt descent, respectively. There was no threshold temperature above which the run started. The smolts started to descend at temperatures between 5.8–11.2°C. Jonsson and Ruud-Hansen (1985) concluded that the timing of the smolt descent in the River Imsa was not triggered by a specific water temperature or a specific number of degree-days during spring, but it was controlled by a combination of actual temperature and temperature increase in the water during spring. The smolt run started early in years when the water temperature in spring was high or when the increase in temperature was rapid, and it started later in years when temperature conditions were the opposite. Similarly, Holtby et al. (1989) found that variability in stream temperatures during the spring of 9 consecutive years accounted for 60 % of the variability in the mean date of coho salmon smolt emigration in Carnation Creek, British Columbia. Solomon's (1978, 1982) investigations of brown trout smolts also indicated that time of descent was correlated with the increase in water temperature in spring. Bjornn (1971) studied the trout and salmon movements in two Idaho streams. The volume of flow in the streams fluctuated within a narrow range. Peak movement in spring of steelhead trout and chinook salmon occurred during stable or decreasing water flows. However, the smolt migrations of both the salmon and trout species coincided with increasing stream temperature in the spring.

In rivers without spring freshets the timing of smolt descent is probably linked to the timing of the smolting process. The increasing photoperiod in spring appear to be the major environmental variable that affect the onset of the smolting (McCormick et al. 1987, Okumoto et al. 1989), but this timing is also affected by variations in water temperature (Clarke et al. 1981, Johnston and Saunders 1981, Zaugg 1982, Dickhoff et al. 1989). The dependence on photoperiod secures that the process of smolting occurs during spring. Variations between years, however, are influenced by differences in water temperature. As the duration of the daylight is the same on the same day each year, photoperiod cannot cause any variation in time of smolting. The annual variation in smolting may thus be reflected in the timing of the smolt run as described above.

The water temperature may also be important for the start of the spawning migration of silver eels downstream rivers and their rate of river descent. Vøllestad et al. (1986) found that the number of descending silver eels and the start of the downstream migration in River Imsa varied between years. The run started earlier in years with low than in years with high water temperature during July and August. Furthermore, they found that most silver eels descended at temperatures between 9 and 12°C. The recapture rate of silver eels transplanted within River Imsa was highest at 9°C and decreased at both higher and lower temperatures ($r^2=0.95$). Few silver eels descended at temperatures above 18°C or below 4°C. But, although water temperature significantly influence the start of the run, Vøllestad et al. (1986) found no threshold temperature at which the run started as suggested by Tesch (1977).

Upstream migration

In rivers with small fluctuations in water levels during the migratory period, water temperature appears to be an important factor stimulating upstream fish migration. For instance, importance of increasing water temperature for the ascent of elvers has been noted by several authors (e.g. Sörensen 1951, Gandolfi et al. 1984, Hvidsten 1985, Sörensen and Bianchini 1986, Naismith and Knights 1988, Vøllestad and Jonsson 1988). In River Imsa, the annual number of ascending elvers of European silver eel was positively correlated with water temperature (Vøllestad and Jonsson 1988). In the River Arno, Italy, on the other hand, differences in temperature between sea and river water seem to play an important role in the ascent of elvers (Gandolfi et al. 1984). Marked migratory movements occurred when river and sea water showed differences in temperature not exceeding ±3–4°C. Movements decreased when temperature difference in either direction was greater.

Water temperature in rivers appears also to stimulate the spawning migration of many species. Davies and Sloane (1987) studied the upstream migration of spawning brown trout and rainbow trout in Liawenee Canal, Great Lake, Tasmania, 1949–85. They found that brown trout migrated upstream from early April to mid May and rainbow trout from late August to early November. Brown trout migrated predominantly over the temperature range 6–10°C, while rainbow trout migrated mainly over 5–11°C. Furthermore, rainbow trout migration occurred at high flow conditions and was positively correlated with canal flow increases, whereas brown trout migrate during low canal flow. Some authors have found that the upstream migration starts above a threshold water temperature or at preferred temperatures. According to the literature, these temperatures vary within and among species (Sörensen 1951, Matsui 1952, Bigelow and Schroeder 1953, Smith 1955, McKenzie 1964, Rembiszevski 1970, MacLean and Gee 1971, Kuznetsov 1976, Leggett 1976, Malmqvist 1980, Gandolfi et al. 1984, Helfman et al. 1984, Hvidsten 1985, Sörensen and Bianchini 1986, Hutchinson and Mills 1987, Naismith and Knights 1988). Fish are poikilothermic animals and their activity are dependent on the temperature in the water. At low temperatures they are less active than at higher temperatures. On the other hand, the activity at higher temperatures require higher energetic costs. Thus the upstream migration is expected to occur at temperatures above a minimum, but not at too high temperatures. For instance, at low temperatures upstream migrating fish may have problems with passing obstacles. Jensen et al. (1989) found that Atlantic salmon were unable to pass waterfalls in the River Vefsna if the water temperature was below 8°C. An example illustrating how high water temperature may decrease the intensity of upstream migration was published by Elson (1969). When studying the intensity of Atlantic salmon migration in the Northwest Miramichi River he found that the ascent increased with increasing water temperature up to 24–25°C (the lethal upper temperature limit is about 30°C) and then decreased. Hawkins (1989) noticed that when water temperature in River Dee, Scotland, exceeded 20°C the fish remained in the sea. Furthermore, MacLean and Gee (1971) observed that brook stickleback, *Culaea inconstans*, in Roseau River, Manitoba migrated upstream in water velocities less than 90 cms^{-1} and when a temperature gradient (15.6–21.1°C) was present.

Water flow and temperature

Hierarchy or alternatives

Water flow and water temperature stimulate both up- and downstream migration of fish, and they appear to trigger the same behaviour in different rivers. For instance, the downstream migration of smolts in River Orkla was initiated by the increasing water flow in the river (Hesthagen and Garnås 1986), whereas in River Imsa the smolt run was initiated by the increasing water temperature and not by increasing water flow (Jonsson and Ruud-Hansen 1985). Furthermore, in some eel species the upstream migration of elvers coincide with increasing water flow (Jellyman and Ryan 1983), whereas in others the ascent of elvers was correlated with increasing water temperature in the river (Vøllestad and Jonsson 1988). These differences may be explained in two ways. First, there may be a hierarchy of environmental factors stimulating the fish migration in rivers. Hypothetically, if the spring flood in River Orkla was left out one year, increasing water temperature might trigger the smolt migration, which would then occur later in the season. Næsje and Jonsson's (1988) laboratory study on hatching whitefish eggs, appear to function this way. Whitefish eggs may hatch early or late during the ontogeny when exposed to varying environmental stimuli. When the eggs were agitated by moving water they hatched at an earlier developmental stage than when agitation was left out and water temperature determined hatching time. A second explanation may be that the time of migration is adapted to different environmental factors in different rivers. For instance, the smolt migration may be triggered by increasing water flow in some rivers and increasing water temperature in others. Results from the two Norwegian rivers, Imsa and Orkla, appear to support this second explanation. In Imsa, the smolt migration is triggered by increased water temperature in spring. In 2 out of 8 years, however, there was a spring freshet just prior to the regular time of seaward smolt migration without any observable effect on downstream movement of the fish (Jonsson and Ruud-Hansen 1985). In Orkla, on the other hand, the migration was annually initiated by the increase in spring flood (Hesthagen and Garnås 1986). This implies that different mechanisms may function in different rivers depending on adaptations to local environmental factors, securing that the migration starts at the right time to maximize the profitability of the migration.

Light

Downstream migration

Numerous authors have found that downstream migrations of fish occur mainly during darkness (e.g. Cope 1956, McDonald 1960, Northcote 1962, Geen et al. 1966, McCart 1967, Mason 1975, Sjöberg 1980, Tuunainen et al. 1980, Solomon 1982, Youngson et al. 1983, Muth and Schmulbach 1984, Hansen and Jonsson 1985, Haraldstad et al. 1985, Næsje et al. 1986, Irvine 1986, Corbett and Powles 1986, Vøllestad et al. 1986, Johnston and Cheverie 1988, Thorpe et al. 1988).

Moonlight or artificial light reduce the downstream movement of salmonid fry (Northcote 1962, Geen et al. 1966), and in long streams, when the migration is not completed in a single night, the fry occupy holding areas during daylight (McDonald 1960, Hartman et al. 1962). Mason (1975) studied the seaward migration of coho salmon and found that the peak movement coincided with the new moon and progressively declined within case of four lunar cycles.

Illumination of the river during night reduces the migration speed of smolts. Hansen and Jonsson (1985) studied the downstream migration of hatchery reared Atlantic salmon smolts in the River Imsa, Norway, released at different times of the day. They found that smolts released in the evening descended faster than smolts released in the morning. However, large numbers of hatchery smolts released in the morning schooled downstream during daytime. In such cases a number of wild smolts joined the schools opposite to the usual situation with night descent. The reason may be that the schools offer predator defence (Pitcher 1986) acceptable for wild smolts. The releases were made after the majority of wild smolts had moved to sea.

Laboratory studies on the activity rhythms of downstream migration of river lamprey showed that emergence from the substrate and swimming were primarily nocturnal, with a maximum in free-swimming activity at the onset of darkness and a smaller activity peak at the transition from the dark to light phase (Potter and Huggins 1973). During the light period these animals showed a significant preference for burrowing or lying in regions of gravel and pebbles.

Silver eels migrate downstream during night, and the migratory activity depends on the light intensity (Deelder 1954, Burnet 1969, Todd 1981, Haraldstad et al. 1985, Vøllestad et al. 1986). In Dutch inland and Baltic waters the maximum activity of silver eels occurred around the last quarter of the lunar cycle (Frost 1950, Lowe 1952, Jens 1952/53), while in the Upper Rhine maximum activity occurred before the moon's last quarter (Jens 1952/53). Boëtius (1967) and Edel (1976) showed that silver eels held in tanks in complete darkness with constant temperature and water flow, had an innate activity rhythm correlated with lunar phase. Vøllestad et al. (1986) studied the effect of light on the migratory activity of European silver eels in River Imsa, Norway. They placed two lamps at a weir in the river. Light intensity measured at the darkest point across the river was approximately 0.15 lux when light was on and approximately 0.007 lux when light was off. They found that during 29 half hour periods of illumination, 81 silver eels were caught. During the intervening dark periods, 362 silver eels were caught. Furthermore, during nights with moon light they found that most silver eels descended during the first dark period after sunset when light intensity was less than 0.06 lux, and stopped when the moon appeared above the horizon and shone on the river. Burnet (1969) and Todd (1981) also registered minimum catches of silver eels during full moon, but activity occurred during more than half the lunar period.

The above findings show that the migration activity of silver eels is influenced by variations in light intensity. The innate lunar-correlated activity rhythm may only be expressed when eels are deprived of other sensory inputs. In nature, however, apparent lunar-correlated activity is probably caused by variations in light intensity, and not by variation in moon phase per se.

However, migrating fish have been observed during daytime. For instance in turbid water pink and chum salmon have moved downstream during day (Hoar et al. 1952, MacKinnon and Hoar 1953, Neave 1955, Coburn and McCart 1967). In some rivers the wild smolts appear regularly to migrate during daytime. At high latitudes in areas with midnight sun, smolts of Atlantic salmon and brown trout have been observed migrating during hours of strong sunlight (Thorpe and Morgan 1978 and references therein). In the north Swedish River Rickleå, Österdahl (1969) observed a change from nocturnal migration pattern in late May and early June to diurnal pattern in late June. Österdahl (1969) did not give the length of the night during the smolt migration, but at 64°N the nights in May/June are short, and it never gets really dark. However, even further south day-time migration may occur. Solomon (1978) found that in River Piddle, large numbers of Atlantic salmon smolts migrated at bright sunlight mainly between 14:00 and 18:00 hours, while the smolt of brown trout had a definite peak of downstream movement in the early hours of darkness (21:00–24:00 hours).

The migration occurs probably at the time of the day when the survival is expected to be highest, and movement during night is probably an adaptation to avoid visual predators. Visual predators, however, may also be avoided during daytime. For instance, Bakshtansky et al. (1976, 1977) maintain that the pike (*Esox lucius*) in the rivers Porje and Soyana had difficulty capturing smolts in sunny weather, when light ripples occurred on the surface of shallow water. In these rivers smolts migrated during day time.

Upstream migration

Usually fish migrate upstream mainly during twilight and dark periods. For instance, elvers ascend freshwater during dark hours (Jellyman and Ryan 1983, Gandolfi et al. 1984, Tzeng 1984, Sörensen and Bianchini 1986, Potter 1988). The upstream migrating river lamprey occurred mainly at nights with no moonlight (Potter and Huggins 1973, Asplund and Södergren 1975, Malmqvist 1980, Sjöberg 1980). In Atlantic salmon and kokanee (*Oncorhynchus nerka*), Hellawell et al. (1974), Potter (1988) and Lorz and Northcote (1965) observed that most movement occurred during hours of darkness. The majority of kokanee entered Moore Creek early in the evening so that the migration was virtually ended by midnight. In Lake Pounui, on the other hand, twilight activity of elvers occurred. In January, maximum river ascent occurred at 22:00 and 04:00 hours, whereas in April, maximum activity occurred at 21:00 and 07:00 hours (Jellyman and Ryan 1983). The activity periods were more spread in April, probably reflecting the longer period of darkness. Some species, however, migrate during daytime. MacLean and Gee (1971) observed greater upstream movement of prespawning brook sticklebacks during day than night. In most species, however, daytime migration occurs under special conditions. For instance, when large amount of elvers moved upstream (more than 5,000 elvers per day), Jellyman and Ryan (1983) observed that some elver movement were normally during day. In turbid water during floods, Hellawell et al. (1974) observed upstream migrating salmon during daytime. Likewise, Potter (1988) observed that Atlantic salmon entered the river during day time at very high flows. Malmqvist (1980) observed day migrating lamprey late in the spawning season. In such cases there is probably no survival premium on night time migration.

Active and passive migrations

Migrations go both up- and downstream rivers. There is no disagreement about that upstream migrations are active, whereas it has been debated whether downstream migrations are active or passive (e.g. Neave 1955, Northcote 1962, Solomon and Templeton 1976, Potter 1980, Solomon 1978, 1982, Thorpe et al. 1981, Thorpe 1982, McDowall 1987).

The passive component in downstream migrations may be that water flow is the vector that displaces the fish downstream. There would be energetically inefficient for the fish to swim actively downstream when the water flow passively transport them over the same route. Furthermore, Hoar (1953), Northcote (1962) and Lindsey and Northcote (1963) argued for passive displacement of downstream migrating fish. Hoar (1953) maintained that chum salmon larvae (*Oncorhynchus keta*) might drift passively downstream during night because they loose their rheotactic response during darkness. Northcote (1962) indicated that rainbow trout may drift downstream at night because of lost visual orientation. Lindsey and Northcote (1963) argued similarly for why larvae of redside shiners (*Richardsonius balteatus*) drifted downstream at night.

However, there must be active components in downstream migrations. For instance, the fish has to decide when to start their downstream migration. Næsje et al. (1986) found that the outdrift of newly hatched larvae of cisco and whitefish in the Norwegian River Gudbrandsdalslågen occurred mainly at nights. In a laboratory experiment with whitefish Næsje and Jonsson (1988) found that eggs hatched at the same rate during light and dark hours, indicating that newly hatched larvae decide when to emerge and raise from the substratum and start their downstream journey to the lake where they start external feeding. Furthermore, since salmonid smolts in most rivers migrate during night but not during daytime, there has to be periods when the fish actively resist the water current and stay close to the bottom and periods when they allow the water flow to displace them downstream (Solomon 1978, Hansen and Jonsson 1985). Another active component probably is that descending fish actively avoid obstacles and backwaters in the river. Release experiments with oranges were done in River Imsa to estimate the rate of passive transport (Hansen and Jonsson 1985). More than 80 % of the oranges were stopped by obstacles in the river and never reached the river mouth. The active component in the downstream migration is also indicated in situations when the displacement occurs concurrently with a rise in water temperature. As described earlier, this may be the case among descending salmonid smolts, but may also occur when older ontogenetic stages migrate downstream as in Arctic charr in River Imsa (Jonsson et al. 1989). Furthermore, Arawomo (1981) found that increasing water temperature accelerated the pace of migration of brown trout into Loch Leven, Scotland, in spring.

All in all, there is probably both active and passive elements in the downstream migrations, where the water current is the vector which brings the fish downstream, when the fish actively have to move into the current and stay there.

Conclusions

1. Water flow, water temperature and light are environmental variables influencing when the fish migrate and the intensity of the migration. These variables apply both to up- and downstream migration, but different variables may trigger the same behaviour in various rivers.

2. In some rivers changes in the water flow initiate the downstream migration of fishes, e.g. salmonid smolts and silver eels. The water flow is the vector transporting the fish downstream. It also appears to influence on the direction and the speed of migration. Migration during high flow may provide shelter for the fish, because rivers are often turbid during high flows and the water surface form ripples.

3. High water flows appear to be an important factor stimulating upstream migration of various fish species, especially in rivers with highly fluctuating water levels during migration periods. Furthermore, high flow may aid the fish in finding the mouth of the stream they are going to enter. Very high water discharges appear to temporarily stop the upstream migration of some fish species. High water discharge during upstream migrations may be more essential for large than small salmon. Upstream migration during high flow increases the energetic costs relative to low flow situations. However, the increased cost is probably balanced by the increased protection offered by the increase in flow.

4. Water temperature is an important factor initiating downstream fish migrations, especially in rivers when freshets do not regularily occur simultaneously with the time of downstream movement. There is probably no threshold temperature starting the smolt run, but a combination of actual temperature and temperature increase in the water during spring. Water temperature is also important for the rate of river descent. The fish are poikilothermic animals and their activity are dependent of the water temperature. In some species increased water temperature accelerated the pace of migration.

5. In rivers with small fluctuations in water levels during the migratory period, water temperature appears to be an important factor stimulating upstream migration of various life history stages of fish. However, very high temperature may temporarily stop upstream migration.

6. Water flow and water temperature stimulate up- and downstream migration of fishes, but appear to trigger different behaviours in different rivers. In some rivers the upstream migration of elvers of several species of eels coincides with increased water flow, but with increased water temperature in others. This may be explained in two ways: (1) that there is a hierarchy of environmental factors initiating fish migration, (2) that the time of migration is adapted to different environmental factors in different rivers. There are results supporting both views.

7. The up- and downstream migrations mainly occur during darkness. Moonlight or artificial light reduce the downstream movement of fish. Migrating fish have been observed during daytime. At high latitudes in areas with midnight sun, smolts have been observed migrating during hours of sunlight. Furthermore, turbid water during floods and during large movement of fish, migration during daytime has been observed.

8. The upstream migrations of fish are active, whereas it has been debated whether downstream migrations are active or passive. The passive component in downstream migration may be that water flow is the vector that displaces the fish downstream. One active component may be that the fish has to decide when to start their downstream migration. Another is probably that the descending fish actively avoid obstacles and backwaters in the river.

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Stationarity and Homing Ability of Landlocked Arctic Charr

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Abstract

A prerequisite for the segregation of fish into distinct populations is that they have the ability to return to a distinct "home area" after displacement (homing). The homing ability of Arctic charr (*Salvelinus alpinus*) was examined by conducting mark-recapture experiments in Lake Takvatn, a 15 km^2 lake in North Norway.

Capture and marking was carried out at four stations. The distance between stations varied from 2 to 7 km. Groups of charr were caught using a small beach seine and marked by fin clipping. Charr were marked and released at the site of capture. Approximately the same number of charr were caught at three stations and transferred to another site and released. Distances between capture and release sites were 2.6, 4.6 and 6.4 km. The following year, during the ice-free season, all four stations were sampled monthly for marked fish.

The results suggest that the charr living in the littoral zone show a high degree of stationarity. The charr also showed the ability to home when displaced to other sites. Homing success appeared to increase with increasing fish size.

Introduction

Arctic charr (*Salvelinus alpinus*) occur in a variety of forms, differing in both morphology and life history patterns. The variety of ecological situations in which charr are found testify to the adaptability of the species (Maar 1949, Nilsson 1955, Frost 1963, Nyman 1967, 1972, Nilsson and Filipsson 1971, Nyman and Filipsson 1972, Skreslet 1973, Klemetsen and Grotnes 1975, 1980, Henricson and Nyman 1976, Behnke 1980, Johnson 1980, Hindar and Jonsson 1982). The numbers of different morphs recorded throughout the geographic range of the Arctic charr has given rise to discussion as to whether "the *Salvelinus alpinus* complex" constitutes closely related, but distinct, species or not (McPhail 1961, Behnke 1972, McCart 1980, Skreslet 1973, Nordeng 1983).

By definition, sympatric populations are reproductively isolated by dissimilarities in genetic and behavioural characteristics, but the distinction between sympatric populations must be moderate, otherwise they would be defined as discrete species.

Coexistence of such forms within a species may be expected in cases where populations have been introduced from separate sources of origin. Dissimilarities in the source habitats could easily provide the basis for differences in the use of resources by introduced populations. Thus, in some cases where sympatric charr are found, they could have had allopatric origins (Klemetsen and Grotnes 1975, Nyman 1972, Nyman et al. 1981). This would not, however, apply to lakes where there is only one population source and where repeated invasions are unlikely (e.g. Lake Ellasjöen, Klemetsen et al. 1985). Comparison of different forms or morphs, living in dissimilar environments, but originating from the same genetic pool, could reveal important traits of phenotypic and genetic ability for environmental adaptation. Ecological segregation into distinct populations in a lake, requires that individuals are able to recognize their "home area", and also prefer to remain there, i. e. they show what can be termed "stationarity".

Charr were introduced into Takvatn, a lake in North Norway, from a nearby lake, Fjellfrosvatn, during the early 1930s (Svenning 1985). The environmental conditions in the two lakes are dissimilar and the two charr stocks are now morphologically distinct. Takvatn has an area of 15 km^2 and is sufficiently large to offer a variety of ecological conditions and several separate spawning areas. Since the charr in Takvatn, have become

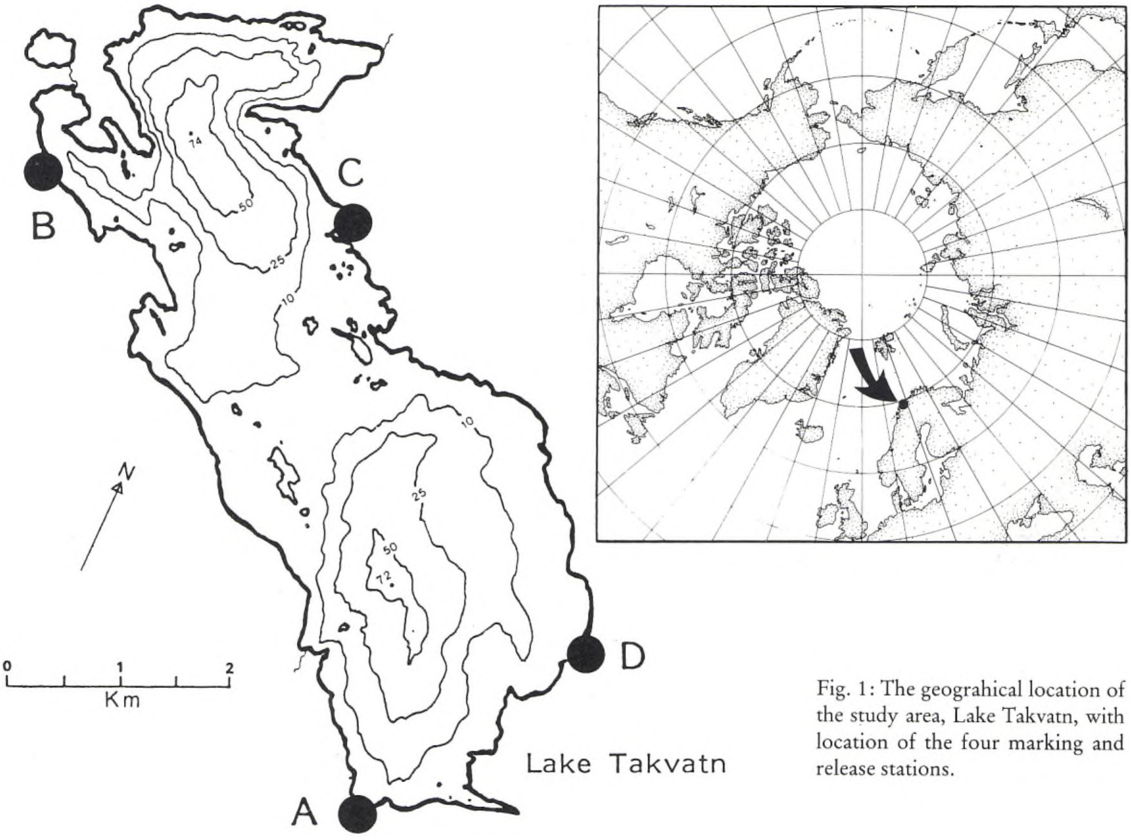

Fig. 1: The geograhical location of the study area, Lake Takvatn, with location of the four marking and release stations.

morphologically distinct from the parent stock (Fjellfrosvatn) in the time span of only 8 generations, it is possible that a number of different morphs could also be developing within Takvatn. A high density of slow growing charr in Takvatn (Aass 1978) implies a strong competition for resources, conditions under which specialization in habitat usage would be expected (Savvaitova 1980).

Frost (1965) has shown that charr repeatedly return to spawn within a given area. Charr therefore have the ability to perceive, within a lake, a "home" spawning area, similar to what is known for the river spawning salmonids. A similar perception of a distinct habitat, if it existed, could act as a factor governing allocation of food resources between morphs. The experiment reported here is a contribution to the ecosystem analysis of Takvatn. It concentrates on the question of whether charr are able to discriminate between areas and perceive a distinct home area. Habitat fidelity was examined by marking, displacement and recapture experiments in Takvatn.

Material and methods

Takvatn is an oligotrophic and dimictic lake in North Norway (Kildemo 1982). The area of the lake is approximately 15 km^2. There are two main basins, and both have a maximum depth of about 70 m. The basins are separated by a shallower area which is less than 10 m deep (Fig. 1). The ice free season lasts from June to November.

Prior to 1930 brown trout (*Salmo trutta*) was the only fish species in Takvatn. Exploitation reduced the trout population, and charr (from a nearby lake, Fjellfrosvatn) was then introduced (Svenning 1985). In 1950 stickleback (*Gasterosteus aculeatus*) was introduced. Investigations con-

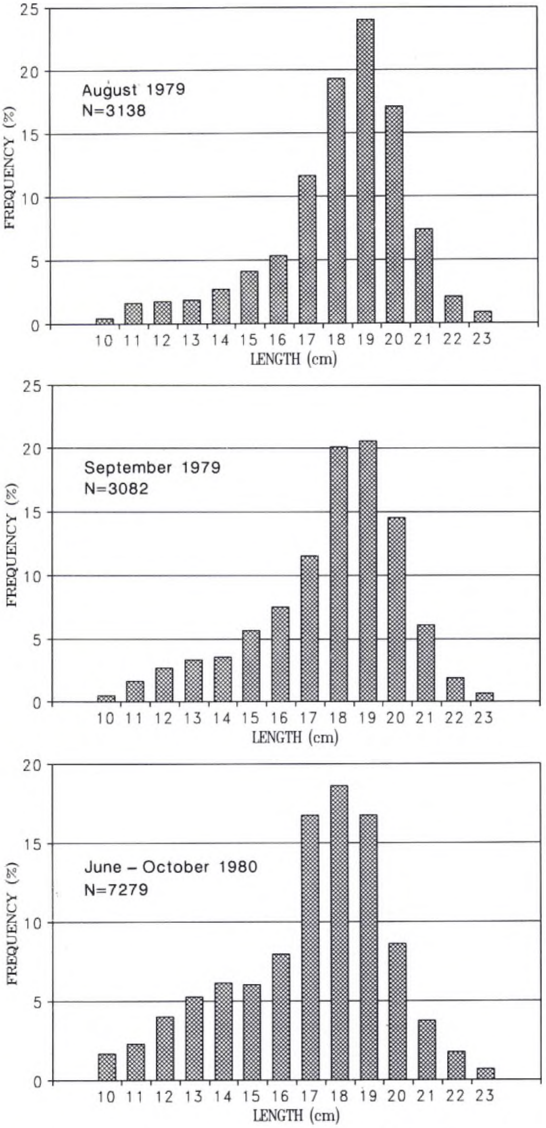

Fig. 2: Length distributions of seine samples of Arctic charr from Lake Takvatn – in August 1979, September 1979 and from June to October 1980.

ducted during the late 1970s (Aass 1978) showed that the charr in Takvatn were stunted, slow growing fish in poor condition, with white flesh, and heavily infected with *Diphyllobothrium* spp.

In 1979 charr were marked and released at four different stations, two in each basin (Fig. 1). None of the stations were spawning areas. The distances between the sites within each basin were 2.1 and 2.6 km, and the sites in different basins were 4.6 to 6.4 km apart. Salted lumpfish roe (*Cyclopterus lumpus*) was spread as bait at the stations approximately 12 hours before fishing with a 30×6 m beach seine (mesh size 10 mm). Landings of charr varied, but successful hauls contained several hundred fish.

In total about 6,000 charr were marked by fin clipping using a series of patterns which allowed fish to be identified by marking site and date. Marking and releasing was carried out twice, in periods a fortnight apart. On the first occasion, in August 1979, five hauls were taken at each site, and about 3,000 charr were marked and released where caught (Fig. 2). Five beach seine hauls were also taken at each site in September, and about 3,000 fish were marked, transferred from their home sites, and released at the station designated as site C (Fig. 2). Seine samples were taken during August/September 1979; and monthly the following year, from June to October. Samples were taken at all stations (A–D) and checked for recaptures. Two hauls were taken at each site, during each month from June to October 1980, and the approximately 7,000 charr which were captured, were examined for marks (Fig. 2).

Table 1: Recaptures of charr marked and released in August. The recaptures were made in August/September, within 2–3 weeks after release.

Home site	Released in August	Total captured August/Sept.	Recaptured at home site	Caught at other sites	Proportion caught at home site
A	1,045	1,155	138	13	91.4 %
B	553	563	40	2	95.2 %
D	1,196	1,163	96	19	83.5 %

Table 2: Recaptures of charr marked and released in August. The recaptures were made from June–October the following year.

Home site	Released in August	Total captured August/Sept.	Recaptured at home site	Caught at other sites	Proportion caught at home site
A	907	1,791	155	12	92.8 %
B	513	1,196	52	4	92.9 %
D	1,100	2,826	157	11	93.5 %

Results

Recaptures of fish released where originally caught

During the first three weeks after the initial release, a total of 2,881 charr were caught in the three areas (A, B & D). Of these fish, 308 were recaptures and 274 were caught at the site where they were originally marked (Table 1). Of the 34 recaptured fish which had strayed from the original site of capture and release 21 were caught at site A and 13 at site D. Only 2 of the recaptured charr were not caught in the same basin as released (Table 1).

During the ice-free season, from June to October in the year following marking and release, a total of 5,813 charr were caught in the three areas (A, B & D). Of these, 391 charr were recaptures and 364 of the recaptured fish were caught at the sites where they were originally released (Table 2). The 27 recaptured straying charr consisted of 11 "D-site" charr recaptured at site A, and 12 "A-site" and 4 "B-site" charr caught at site D. Thus only 4 charr were not caught in the same basin as released.

The proportions of fish recaptured was influenced by fish length at release. Less than 1 % of charr under 17 cm length were recaptured, compared to an average of 18.4 % for fish that were larger than 21 cm when marked.

Recaptures of fish transferred and released at site C

During the marking period (10 days) in August–September, 35 charr were recaught at the site from which they were displaced. The first recaptures were at sites A and D – six days after transfer. Thus, these recaptured fish had moved at least 5 km to the original site of capture, within the space of less than one week.

During June to October, in the year following marking and transfer to site C, 7,279 charr were caught. Of the 319 recaptures, 262 were caught at their "home site" (Table 3), and only 19 at the site of release, site C (Fig. 3). Only 23 charr were not recaught in the same basin as originally captured. Charr transferred from site B, which was in the same basin as the release site (site C), had the highest proportion of recaptures (Table 3).

Table 3: Recaptures of charr marked and released in August/September. All fish were released at site C and the recaptures were made from June–October the following year.

Home site	Displaced and released	Total captured June–October the year after	Recaptured at home site	Caught at other sites	Proportion caught at home site	Proportion caught in home basin
A	1,147	1,791	81	28	71.1 %	92.7 %
B	565	1,196	73	5	90.1 %	97.4 %
D	1,169	2,826	108	24	81.8 %	90.2 %

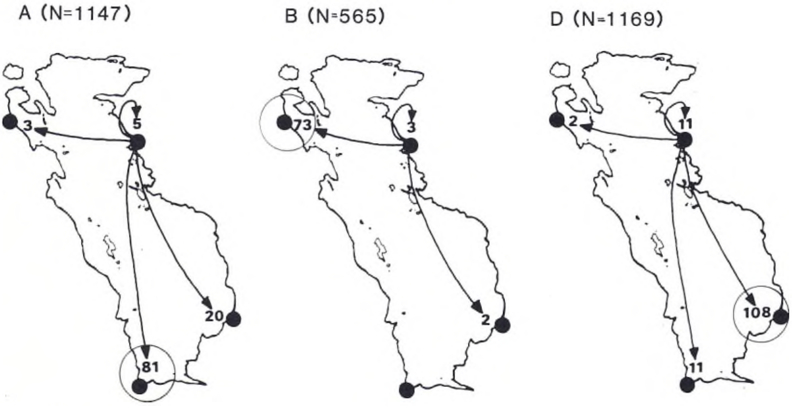

Fig. 3: Sites of recapture for fish displaced from sites A, B and D to site C.

Charr caught at their "home site" were significantly larger than other recaptures (chi-square test, $P<0.01$), and the ratio homers/strayers increased with increasing size of the charr (Fig. 4).

Discussion

The strong homing behaviour of salmonids has been cited as an important element in maintaining reproductive isolation between sympatric forms, and as an attribute that might lead to genetic differentiation (Frost 1965, Svärdson 1970, Behnke 1972, Nyman 1972, Allendorf et al. 1976). Both reproductive homing (returning to the same spawning area each year) and in season homing (returning to the same spawning ground after having been displaced) are behaviours common to charr in several lakes (Alm 1950, Frost 1963, McCleave 1967, McCleave et al. 1977).

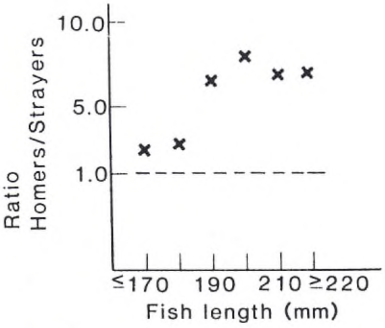

Fig. 4: Ratio of homers (charr recaptured at home site) to strayers (captured at other sites) in relation to fish length.

The best documented case for sympatric charrs is given by Frost (1965) who showed that, in Windermere, there are two forms which differ in both spawning time and place. By mark and recapture experiments it was shown that charr repeatedly and unfailingly returned to the same spawning area, which implies that these charr have a homing ability that could lead to reproductive isolation. Frost (op.cit.) maintained that the difference in spawning time is merely a phenotypic reaction to the differences in environmental conditions at the spawning areas. By implication this would be an example of sympatric populations derived from one, originally homogeneous, stock. Arctic charr lakes with several widely separated spawning areas present the opportunity for fostering discrete populations and in some instances these may be ecologically specialized charr forms (Svärdson 1979, Balon 1980). Occasionally this may provide conditions necessary for the process of sympatric differentiation into morphs and, eventually, species.

Svenning (1985) showed that charr from the two basins in Lake Takvatn, display differences in individual growth and age distributions. This could be due to differences in habitat between the two basins, or be an effect of different intensities of exploitation (Svenning op.cit.). Nevertheless the two basins may contain separate population components, and this appears to be supported by the results of the marking experiment.

It was demonstrated that charr living in the littoral zone tend to have specific "home" areas and, after displacement, the fish had the ability, not only to migrate to their home basin, but, as a rule, to their home site. The displaced charr soon moved away from the site of release and some of the charr traversed the return distance of up to 7 km to their "home" site in less than 6 days.

In Lake Takvatn the littoral zone, with an abundance of large benthic prey, is the most attractive habitat for feeding (Klemetsen et. al. 1989). There is, however, a predation risk, mainly for younger charr, from diving birds (mergansers) and brown trout. Thus the oldest and largest charr would be expected to be more frequently found in littoral zone. This was in accordance with the results from the marking experiments. Recaptures appeared to increase with increasing fish size, suggesting that "stationarity" is related to size and age, with older and mature charr dominating a territory. It must be noted, however, that even small charr were recaught, most of them at their home "site". The tendency therefore appears to be that homing is common to the charr, but that this becomes more pronounced with increasing fish size and age.

The results relating to the "stationarity" of the Takvatn charr are insufficient to claim that the lake contains sympatric populations, but the conditions within the lake may favour this type of segregation. For a species to segregate into different ecological forms both phenotypic adaptive ability and genetic variation must be present. During the few generations that the charr have existed in Takvatn, the environmental conditions within the lake have changed considerably. A lake initially almost devoid of fish has now become a lake housing large numbers of charr. Initial lack of competition, a large variety of habitats and ample areas for spawning of the charr would be expected to promote the realization of genetic variation.

Sympatric differentiation of landlocked charr is probably dependent upon a heterogeneity of lake habitats (Savvaitova 1980), and this seems to be corroborated in a study of the charrs of Lakes Vangsvatn and Lönavatn (Hindar and Jonsson 1982). The nature of the food resources may induce the charr in a lake to segregate into different forms. Nilsson (1965) showed that decreased food supply enhanced the competition between charr and trout leading to distinct differences in diet between the two species. The two charr morphs, or forms, in Vangsvatn (Hindar and Jonsson 1982) show similar differences. On the other hand inter- and intra-specific competition declines in periods when there is a surfeit of food (Nilsson 1965, Klemetsen and Grotnes 1980, Hindar and Jonsson 1982).

During the last decade competition for food has been heavy in Lake Takvatn (Aass 1978, Amundsen 1984). High fish density and the diminishing food supply, both in quantity and quality (Rubach 1985), favor specialization. The change in food resources and reproductive competition may act as delimiting agents for producing discrete niches. Ecological segregation would then be possible.

Segregation could also happen without heterogeneity in the environment. Frost (1965) has shown that for the two charr forms in Lake Windermere, reproductive isolation is maintained because the yearlings are imprinted to the nursery area. If charr from defined home-areas in Takvatn also spawn on grounds close to these areas, this could lead to reproductive isolation and the creation of isolated forms.

During the 1970's and the early 1980's the fishing intensity in Takvatn was very low due to the poor condition of the charr stock. In 1984 a management programme was initiated and during the period from 1984 to 1989 more than 700,000 charr (32 tons) were caught and removed from the lake. This has led to increased growth rate of the Takvatn charr as a result of reduced population density. The average weight of a mature nine-year old Takvatn charr has increased from 88 g in 1979/80, when the marking experiment was carried out, to 421 g in 1990.

If competition for space and food, and possibly also predation risk, were causal factors for the stationarity or segregation in Takvatn, we should expect that the strong homing tendency demonstrated in our experiment should now break down due to the reduced population density. Some results obtained in 1988 seem to support this, but a large scale mark-recapture program is required in order to provide an adequate test of the hypothesis.

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The Estimation of Pelagic Fish Density, Single Fish Size and Fish Biomass of Arctic Charr (*Salvelinus alpinus* (L.)) by Echosounding

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Abstract

Qantitative echosounding has been carried out in the ultraoligotrophic lake Atnsjøen, SE Norway, to describe pelagic fish density, depth distribution and single fish size along selected transects during the years 1985–90. The pelagic fish density varied between 53 and 285 fish ha^{-1}. As Arctic charr (*Salvelinus alpinus* L.) clearly dominated in pelagic gillnet catches, it is assumed that reflected echosignals mainly represent the pelagic part of the Arctic charr population. Target strength of received signals strongly indicated a pelagic habitat behaviour in upper water strata for fish from size c. 6 cm up to 30 cm. Pelagic fish biomass was estimated to be 9–14 kg ha^{-1}.

Introduction

In Scandinavian mesotrophic and eutrophic lakes, several echosounding investigations has been carried out using the SIMRAD EY-M equipment to estimate density of pelagic fish communities dominated by coregonids, osmerids and cyprinids (Lindem 1979, 1982, Brabrand 1986, Jurvelius et al., 1987, Bjerkeng et al. 1991). However, in the ultra-oligotrophic part of the trophic scale, few echo sounding investigations has been carried out. In Norway these lakes are in the north or in alpine areas and are often dominated by Arctic charr (*Salvelinus alpinus* L.). In such lakes they occur alone or with only a few planktivorous competitors and therefore can also dominate when these lakes are going through the process of eutrophication. Thus, to cover the whole trophic scale, and to investigate the reliability of the echo sounding method in low productive systems, studies were carried out in ultra-oligotrophic Lake Atnsjøen.

Arctic charr is predominantly a planktivorous species (Svärdson 1976). However, there are few investigations concerning young stages of Arctic charr, due to sampling problems (Johnson 1980). During their first year of life, a sublittoral and profundal habitat selection are indicated by Kircheis (1976) and Svärdson (1976) in temporate lakes, while in Arctic lakes, young charr has been observed in the littoral zone (Johnson 1976). The competition between young brown trout and Arctic charr is indicated by habitat shift when they co-occur. In this case, brown trout occupies shallow areas and Arctic charr is more restricted to deep waters (Svärdson 1976, Hindar and Johnson 1982, Jonsson and Graven 1985), reflecting the more aggresive behaviour of 0+ brown trout compared to 0+ Arctic charr as documented by Nilsson (1963). When living alone, reduced competition allows Arctic charr to utilize more rich areas in the littoral zone, clearly demonstrating the importance of fish community for the spatial distribution of fish.

In Lake Tingvallavatn, Iceland, Arctic charr is by far the most dominant fish species. In this lake 0+ Arctic charr with a body length of 42 mm, were caught with a pelagic trawl in September at 15 m depth. At the same time and in the same depth, fish observed by echosounding with target strength corresponding to fish size 30–50 mm were recorded (Sandlund et al. 1988). Littoral areas are also an important habitat for 0+ Arctic charr in this lake, although gillnetting caught no fish younger than 2+ either in pelagic or littoral areas (Sandlund et al. 1987, Sandlund et al. 1988), clearly illustrating the general sampling problems assessing small pelagic fish.

The aim of the present study has been to estimate pelagic fish density, single fish size, and to calculate pelagic fish biomass. It was of special interest to document the presence of small pelagic fish, i.e. yearlings, since this age group is of great importance for lake metabolism, and for the evaluation of fish habitat utilization and species segregation.

Study area

Lake Atnsjøen, situated 701 m a.s.l., is the largest lake in the Atna tributary system (5 km^2 surface area). The greatest depth is 80.2 m. The lake is ultra-oligotrophic, with total phosphorous concentration usually below 10 $\mu g/L$ and alkalinity varying between 60–115 $\mu eqv.L^{-1}$ (Blakar 1989). The maximum epilimnetic summer temperature in 1987 was approx. 12°C, with a diffuse thermocline due to wind exposure (Tvede 1989).

In Lake Atnsjøen, Arctic charr (*Salvelinus alpinus*), brown trout (*Salmo trutta*), minnow (*Phoxinus phoxinus*) and miller's thumb (*Cottus poecilopus*) are present. In the pelagic zone, Arctic charr is the dominant planktivorous fish species while some brown trout also display pelagic behaviour, both planktivorous and piscivorous. The fish yield in 1985 was estimated to be 5.5 kg ha^{-1} (Nashoug and Hegge 1988).

Material and methods

In the pelagic zone of Lake Atnsjøen, echo signals from single fish were recorded with a SIMRAD EY-M echosounder. The working frequency of the system is 70 KHz, and the duration of the transmitted pulse is 0.6 ms, giving a depth resolution of about 0.5 m. The echo signals are shifted down from 70 KHz at the calibrated signal output, to enable recording of the analogue signal on a high fidelity tape recorder. All data have been recorded with a 40 log R, time varied gain control, TVG, applied to the preamplifier. Echo signals were recorded on magnetic tape and analyzed on a microcomputer according to the method described by Craig and Forbes (1969). A more detailed description of the echosounder is given by Lindem (1979, 1982).

The regression Target strength=$20*\log_{10}$ Fish

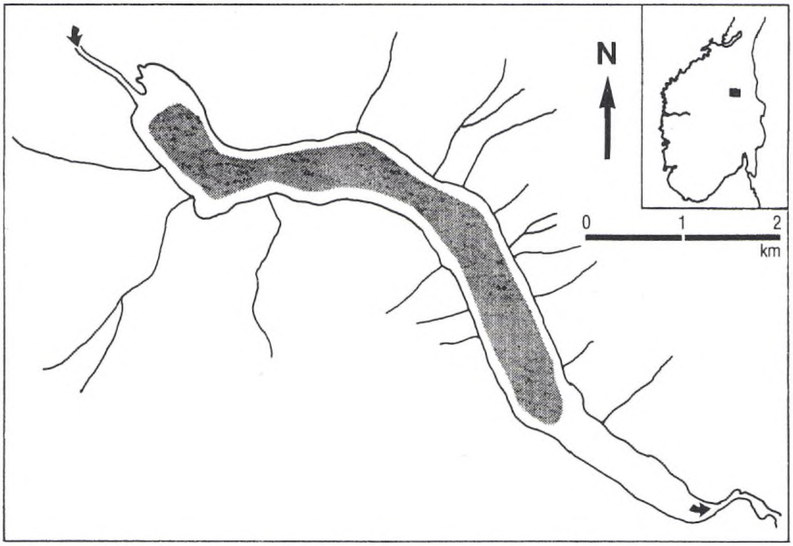

Fig. 1. Map of Lake Atnsjøen. The echo sounding area is shaded.

length-68 given by Lindem and Sandlund (1984) used in earlier echo sounding studies on Arctic charr, has also been used in this investigation. On basis of the number of fish in groups of 2 dB, the total fish biomass along the transects was estimated using the regression $\ln(w) = a \times \ln L - 12.72$ to calculate single fish weight from single fish size (Hesthagen et al. 1989).

Echo sounding recordings were carried out along selected transects (Fig. 1) in late summer 1985 (day), and during autumn 1986–90 (night). Due to low fish density, and no observed regional difference between different parts of the lake, it was decided to analyse the different transects as a unit within each year in the biomass estimation. The analysis for total fish biomass estimation was carried out separately for each water depth interval where fish density was nearly homogenous. The error of the calculations of fish density from the "sampled" volume to surface lake area will then be as small as possible.

The echo sounding method does not observe fish close to the lake surface. In the calculations a "dead" zone is assumed from the surface down to 2 m depth. To compensate for this in the estimation of total fish biomass, water strata down to 2 m were given a similar fish density to the water strata 2–12 m below the transducer. This density is probably a minimum value, as gillnet catches showed higher values closer to the lake surface than in deeper water strata (Hegge 1988, Hegge et al. 1989).

Results

Low fish densities were observed in all years. On the basis of echograms, no regional differences in fish density were observed horizontally along the transects, either during the day or night, although there were indications of a somewhat higher fish density in the southern part of the lake during 1986.

All the observed fish in three fish size groups along the transects during the five years are given in Table 1. The observations include both "small" and "large" fish in all years, represented by target strength of received echosignals of dB -54/-52 and dB -38/-40/-42, respectively. As this last dB group occurred regularly in high numbers all years, this is probably the adult part of the Arctic charr population, with single fish larger than c. 30 cm.

In 1985 dB values corresponding to fish larger than 20 cm and below 10 cm were mainly observed. The total number of fish along the transects was estimated to be 90 fish ha^{-1}. However, the recordings were carried out in the daytime in July 1985. In later years recordings were made at night in August/September.

In 1986 fish densities of 137 and 119 fish ha^{-1} were observed along the transect, as this was divided in two parts. In both parts, fish less than 10 cm and larger than 20 cm, were mainly observed. Single fish size close to 30 cm (dB = -38) showed especially high numbers.

Table 1. Estimated fish density in the pelagic zone of Lake Atnsjøen in 1985–90.

Date	Calculated total number of fish ha^{-1}	Number		
		<10 cm	10–20 cm	>20 cm
27.7.85	90	47	0	43
12.9.86	137	102	3	32
12.9.86	119	76	17	26
5.8.87	99	65	4	29
5.8.87	109	24	5	81
5.8.87	285	218	53	14
29.9.88	53	8	18	27
5.9.89	57	18	16	23
28.8.90	109	40	4	65

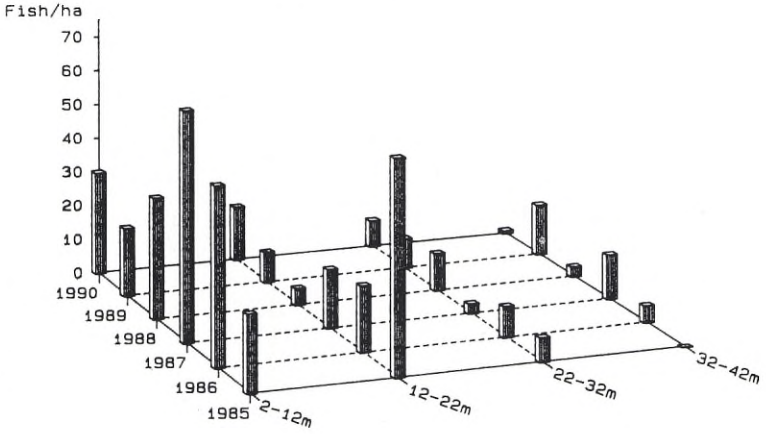

Fig. 2. Depth distribution of the recorded number of fish in 10 m depth water strata in the pelagic area of Lake Atnsjøen in the period 1985–90.

In 1987 the transect was divided into three smaller transects, of which a smaller area showed relatively high densities of large fish, estimated as 81 fish ha^{-1}. However, the total fish density was not especially high. Total fish density along three smaller transects was estimated to be 99–285 fish ha^{-1}, and fish smaller than 10 cm showed high numbers when total fish density was high. The lowest number of fish was observed in 1988 and 1989, with 53 and 57 fish ha^{-1} along the transect as a whole. The estimated number of small fish was also low.

The vertical distribution of fish is given in Fig. 2, showing high fish density in water strata 2–12 m below lake surface during all years except 1985. In this case, the highest number of fish was observed in the depth strata 12–22 m below lake surface. In all years, fish were observed in all water strata analysed.

The total fish biomass along the transects showed values between 9 and 14 kg ha^{-1} (Fig. 3). A standard error of 30 % of the mean for the estimated fish biomass has been assumed on the basis of calculations in a similar investigation (Bjerkeng et al. 1991). In that study an important error source in estimating biomass was the uncertainty in length peak values for single fish within a given target strength interval. Thus a major contribution to the standard error was independent of fish species and lake. It is therefore assumed that the standard error of the estimated fish biomass in Lake Atnsjøen is within the same limits of 30 % of the mean. On this basis there is no significant difference ($P < 0.05$) in the estimated fish biomass in Lake Atnsjøen between years.

Discussion

Catches with bottom gillnets and pelagic floating gillnets showed that juvenile Arctic charr are mainly restricted to benthic areas of the lake, while the adult population was mainly pelagic (Hegge 1988, Hegge et al. 1989). However, smaller

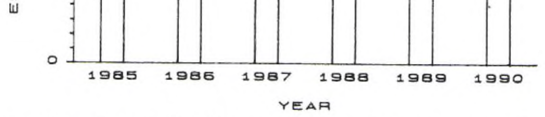

Fig. 3. Estimated fish biomass in the pelagic zone of Lake Atnsjøen, based on target strength/fish size relationship (Lindem and Sandlund 1984) and size/weight relationship Arctic charr (Hesthagen et al. 1989). On the basis of Bjerkeng et al. (1991), a standard error of 30 % of the mean is indicated.

fish than c. 12 cm are not included in the net catches due to smallest gillnet mesh size of 16 mm.

The gillnet results correspond clearly to the main results from the echosounding, as fish larger than c. 30 cm showed high densities/numbers in the pelagic zone. However, single fish with size smaller than approx. 10 cm were also observed with echosounding, in some transects also in high numbers. This contrasts with the gillnet catches in which no fish with a body size smaller than 12 cm were caught (Hegge et al. 1989).

In other lakes dominated by Arctic charr, their juvenile stages show a strong benthic/littoral behaviour, although in all these lakes, few or no benthic/littoral competitors are present (Johnson, 1980). In Lake Atnsjøen, juvenile brown trout are restricted to inlet and outlet rivers, and to some extent to littoral areas. Living sympatrically with Arctic charr, brown trout will usually behave less planktivorous (Brabrand and Saltveit, 1989). Observations of brown trout as a piscivore, feeding on Arctic charr, confirm this niche segregation between Arctic charr and brown trout. However, brown trout in Lake Atnsjøen also feeds on plankton and terrestrial insects. Hegge et al. (1989) showed that brown trout were closer to lake surface than Arctic charr. The habitat selection of young-of-the-year Arctic charr has not previously been documented in this lake. However, the echo sounding results and the fact that some piscivorous brown trout caught by floating gillnets in the pelagic zone had consumed small Arctic charr (size c. 10 cm, Dervo pers. comm.) are strong indications of planktivorous behaviour also in the younger stages of Arctic charr. It must be pointed out that a planktivorous tendency does not exclude a benthic/littoral behaviour. This zone is not available by the echo sounding method.

The vertical net catches in pelagic areas clearly demonstrate higher net catches of both Arctic charr and brown trout above the thermocline (Hegge et al. 1989). Even if the echo sounding method do not include the upper 2 m strata, this corresponds close to the depth distribution observed by echosounding. The depth distribution of fish follows the observed distribution of zooplankton species such as *Bosmina longispina* (Dervo 1988), which is an important food item for fish.

The distribution and estimated fish biomass based on echo sounding data provides an "objective" instantaneous picture of the pelagic fish population, and a measure of fish density and relative size distribution. The estimated total fish biomass was between 9 and 14 kg ha^{-1}. It is obviously a minimum estimate, since the estimated fish biomass is based on fish densities restricted to pelagic areas and gillnet catches were higher close to the lake surface than in deeper waters.

However, the estimated biomass by the echo sounding method seems reasonable compared to other subalpine, oligotrophic lakes. In the Norwegian lake Øvre Heimdalsvatn, Jensen (1977) estimated total fish biomass to be 8.0–19.5 kg ha^{-1} in the years 1958–70 by using a mark-recapture method. In this lake brown trout was the only fish species. The predicted sustained yield of brown trout was calculated to be 5.7 kg ha^{-1} with a mean weight of 269 g (Jensen 1977), giving a factor of 0.8 in the relationship between potential yield, natural mortality and biomass in an unexploited stock (Gulland 1971). The total fish yield in Lake Atnsjøen was estimated to be 5.5 kg ha^{-1} (Nashoug and Hegge 1988) with a pelagic fish biomass of 9–14 kg ha^{-1}. In spite of different fish species, the estimated biomass in the two lakes as well as fish yield is of the same order of magnitude.

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Extinction and Natural Recolonization of Fish in Acidified and Limed Lakes

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Abstract

At least one fish species had been lost in 68 % of the 87 acidified Swedish lakes monitored in this study. The mean number of species per lake decreased from 4.7 to 3.6 and the number of extinct species correlated negatively to mean pH. Among 22 species, European minnow (*Phoxinus phoxinus* (L.)), brown trout (*Salmo trutta* L.), roach (*Rutilus rutilus* (L.)), and Arctic char (*Salvelinus alpinus* (L.)) had high extinction frequencies, whereas northern pike (*Esox lucius* (L.)) and perch (*Perca fluviatilis* L.) had low extinction frequencies. Comparing lakes with four different fish assemblages, the greatest losses were noted in Arctic char lakes, indicating that this type of lakes and fish assemblage is one of the most vulnerable to acidification (85 % had lost one species or more). Roach/pike, whitefish/cisco (*Coregonus* spp./*Coregonus albula* (L.)) and brown trout lakes were less severely affected (50–63 % had lost species) than the Arctic char lakes. On the average, the Arctic char lakes lost 1.7 species per lake, whereas the whitefish/cisco lakes lost 0.7 species. After liming, during a period of 1–18 years, many fish species recolonized and the mean number of fish species in the investigated lakes increased from 3.6 to 4.0. However, in spite of the fact that liming improved water quality (mean pH ca 6.5), the recolonization frequency during this period was not higher than 50 %. Roach, minnow, brown trout, whitefish, northern pike and burbot (*Lota lota* (L.)) recolonized between 25 % and 50 % of the lakes where they had been extinct, but Arctic char did not recolonize any lake. In contrast to the extinction of species, the number of recolonizations did not differ significantly between the four fish assemblages.

Introduction

In Sweden about 16,000 lakes are considered to be severely affected by acidification (Bernes and Thörnelöf 1990). In many of these lakes extinction of fish populations has been reported (Almer et al. 1974, Almer et al. 1978, Almer and Hansson 1980, Johansson and Nyberg 1981, Degerman and Nyberg 1987, Degerman and Nyberg 1989). The main cause of extinction in these lakes and other acidified lakes is recruitment failure due to high mortality rates for eggs, fry and alevins (Leivestad et al. 1976, Almer et al. 1978, Rosseland et al. 1980, Overrein et al. 1980, Gillet and Roubaud 1986). Because susceptibility to acid water varies among fish species, some species die out sooner than others (Almer et al. 1978, Leuven et al. 1987). Susceptibility may also vary between populations within the same species (Rask 1987, Rosseland and Skogheim 1987). Differences in the ionic composition of the water (Leivestad et al. 1976), in the content of humic substanses (Degerman 1987) and in the concentrations of metals such as aluminium, iron and manganese (Andersson and Nyberg 1984, Witters et al. 1987, Hutchinson et al. 1987) may also affect the rate of extinction.

The rate of extinction is further dependent on factors such as population size (Gilpin and Soule 1986), lake size and number of species in the fish assemblage (Magnuson 1976). Small lakes with a large number of species, and consequently also small populations, tend to have a high rate of extinction (Magnuson 1976). Both population size and species richness have been shown to be functions of lake area, lake depth and altitude (Barbour and Brown 1974, Harvey 1981, Tonn and Magnuson 1982, Eadie et al. 1986, Minns 1989, Appelberg et al. 1989). The positive correlation between number of fish species and lake area has also been used to estimate the number of fish population that have been eradicated by acidification (Rahel 1986).

Apart from reducing emission of pollutants, liming is the main measure that can be taken to prevent losses of fish populations and to restore acidified lakes to their original conditions. The general effects of liming the lakes on fish are improved reproduction and increases in population abundance (Eriksson et al. 1983, Nyberg 1984, Matzow et al. 1985, Nyberg et al. 1986a, Nyberg et al. 1986b, Degerman and Nyberg 1989). However, although liming improves water quality, many fish populations do not recolonize limed lakes. In moderatly acidified lakes, Degerman and Nyberg (1989) found a significant increase in the number of species after liming. However, in lakes that had been severly acidified, no significant increase was noted even 5–9 years after liming.

Besides insufficient liming, recolonization may be hindered by migration obstacles (waterfalls, dams etc.), a low ability to migrate, great distance to the nearest potential colonizers, and detramental biotic interactions. According to MacArthur and Wilson (1967), the colonization rate increases as the number of species decreases, the depopulated area increases, and the distance to the nearest pool of colonizers decreases. In lakes and watersystems that have been severly acidified the number of species is low, which would seem to improve the chances for recolonization. However, the extensive extinctions in these water systems means that the nearest colonizer is often guite distant.

The main objective of the present study is to assess the extinction and recolonization frequencies of different species and fish assemblages in acidified lakes, before and after lime treatment.

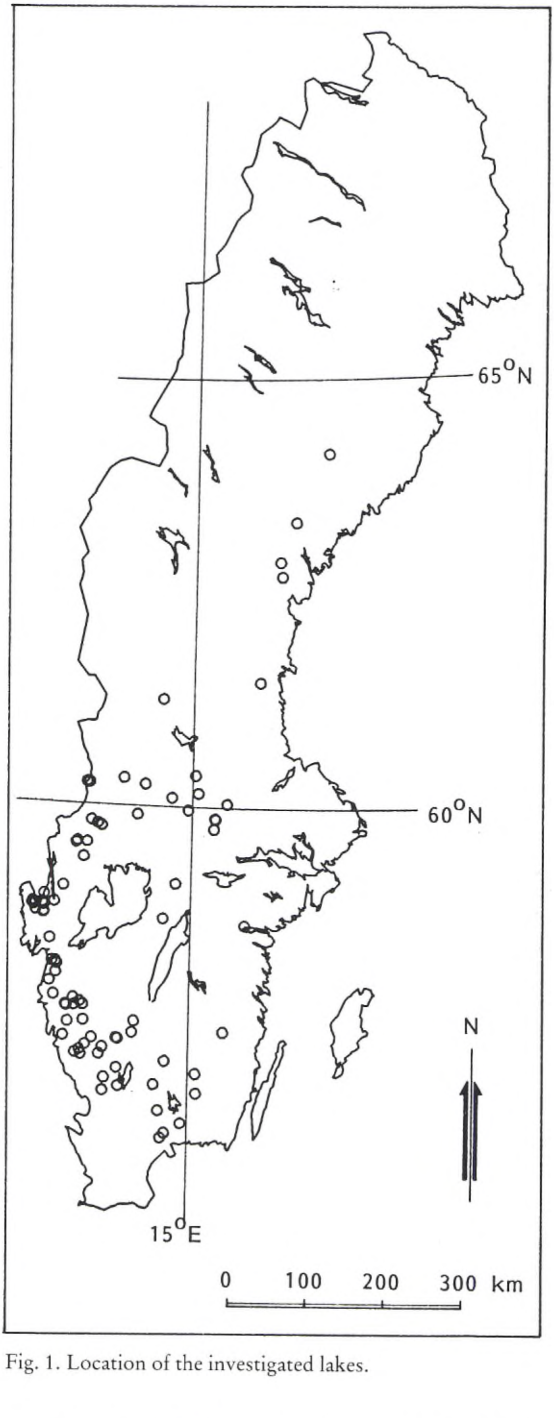

Fig. 1. Location of the investigated lakes.

Material and methods

Selection of lakes

A total of 87 limed lakes were selected from different Swedish national and local monitoring programmes. To be selected, a lake must have been monitored regularly over a long period of time and have had test-fishings conducted at least once before, and twice after liming. For each lake, the sampling programme extended over a 5 to 20 year period. As the acidification of Swedish lakes is most severe in southern and central parts of Sweden, most of the lakes investigated were located in these regions (Fig. 1).

Most of the test-fishings in these lakes were carried out by the Swedish National Board of Fisheries, in conjunction with the Swedish National Environmental Protection Agency, during the period 1971–90. A smaller number of test-fishings were conducted by local county administrative boards or local water owners. In many lakes the test-fishings were conducted several times up to 12–13 years after the first liming. In a few lakes the sampling programme had already been started in 1966–67 and ranged over an 18 year period after the first liming. In all, data from 387 test-fishing occasions were included.

Physical and chemical data, and lime treatment data were obtained from the Swedish Environmental Protection Agency and local county administrative boards. The physical and chemical data included latitude, altitude, lake area, maximum depth, retention time of water, conductivity, water colour and pH. Most of the sampled lakes have been limed several times, some of them annually during the most recent years.

Test-fishing methods

Multi-mesh benthic gillnets were used for the test-fishings, which were carried out once each sampling year sometime between the beginning of May and the end of November. The gillnets used before 1983 were 36 m long and 1.5 m deep and consisted of 12 sections with mesh sizes from 10 to 75 mm. After 1983 the gillnets were 42 m long and consisted of 14 sections with mesh sizes from 6.25 to 75 mm. A standardized gillnetting technique was used in most cases (Nyberg and Degerman 1988, Degerman et al. 1988), and the number and placement of the nets was related to lake area and maximum depth. The gillnetting was depth stratified, with each gillnet randomly distributed over the lake within each depth zone. The number of nets on each sampling occassion varied between 4 and 90.

Lake classification

Based on fish assemblage prior to acidification, each lake was subjectively classified as one of the four types defined and described by Appelberg et al. (1989): 1) Roach/pike lakes, i.e. lakes in which benthic species such as roach (*Rutilus rutilus* (L.)) and northern pike (*Esox lucius* (L.)) dominate, 2) Whitefish/cisco lakes, i.e. lakes in which pelagic fishes such as cisco (*Coregonus albula* (L.)) or whitefish (*Coregonus* spp.) are abundant, 3) Arctic char lakes, i.e. lakes with Arctic char (*Salvelinus alpinus* (L.)) and European minnow (*Phoxinus phoxinus* (L.)), and 4) Brown trout lakes, i.e. lakes in which brown trout (*Salmo trutta* L.) is one of the dominant species. These lake types differed significantly with respect to lake productivity, lake size and altitude (Appelberg et al. 1989). The species *Perca fluviatilis* L. (perch) was present in all four lake types. It was therefore not useful in discriminating between lake types.

Data analysis

The frequency of both extinction and recolonization of fish populations in the lakes was analyzed using test-fishing data and earlier records of fish occurrence (Almer 1972, Almer and Hansson 1980, Dickson et al. 1975, Nyberg et al. 1986b, and unpublished data). A species was considered to be extinct if it was missing in the test-fishing catches and reports from local residents confirmed the species absence. An extinct species was considered to be recolonized if it occurred more than once in the catches after liming.

The data was analyzed using the SPSS-PC+ V3.1 statistical programme (SPSS Inc. 1988). All physical and chemical data used in these analyses, except pH, were normalized using log10 – transformation. Stepwise multiple regression was used to analyse the correlation between physical and chemical data, and number of species prior to acidification. Linear regressions were used to analyse the relationship between species richness, physical and chemical variables, and number of extinct species. In order to test whether or not the selected lake types differed significantly from

Table 1. Lake area (ha), altitude (m) and latitude in the different lake types: 1 = Roach/pike lakes, 2 = Whitefish/cisco lakes, 3 = Arctic char lakes, 4 = Brown trout lakes. N = number of lakes.

Lake type	N	Lake area Median (range)	Altitude Median (range)	Latitude Median (range)
1	27	100 (7– 870)	135 (70–326)	57°40′N (56°50′–60°25′)
2	25	290 (7–3270)	132 (66–267)	57°20′N (56°15′–62°40′)
3	27	122 (15–9540)	225 (85–582)	59°50′N (57°30′–63°20′)
4	8	28 (10– 106)	145 (123–350)	58°55′N (58°40′–64°05′)

each other in terms of physical and chemical characteristics and extinction frequencies analysis of variance (ANOVA) and analysis of covariance (ANCOVA) were used. The change in number of species between unaffected, acidic and limed periods was analyzed using the paired t-test and the Wilcoxon signed-ranks test. The latter was used for the group of brown trout lakes which consisted of only a few lakes. To compare the different lake types in terms of species diversity, Shannon-Wiener's diversity index (H) was used, based on the CPUE (numbers) of fish (Pielou 1969). The change in diversity index between acidic and limed periods was analyzed using Wilcoxon signed-ranks test. The differences in diversity, number of recolonizations, and recolonization time among lake types were analyzed with Kruskal-Wallis one-way ANOVA. The chemical differences after liming, and the differences in number of species and diversity prior to liming, between lakes with and without recolonization were analyzed using Mann-Whitney U test.

Results

Physical and chemical differences between lakes

The lakes sampled have areas ranging between 7 and 9,540 ha, their altitudes are between 66–582 m above mean sea level, and they are situated at latitudes between 56° N and 64° N (Table 1). The maximum depth of the lakes varies between 2 and 86 m, and the retention time of water ranged from 0.1 to 45 years (Table 2). Before liming, most of the lakes had pH values below 6 during the major part of the year, and several lakes had pH values as low as 4.1–4.5 during spring and autumn (Table 3 and 4). The pH of the lake water increased after the lime treatment, and the average pH value was approximately 6.5. However, pH values below 5.0 were occasionally noted.

The four lake types differed with respect to lake area, altitude, depth, retention time, conductivity, water colour and minimum pH (ANOVA, $P<0.05$). However, they did not differ signifi-

Table 2. Lake depth (m) and retention time of water (year) in the different lake types, listed in Table 1.

Lake type	N	Lake depth (m) Median (min–max)	Retention time (year) Median (min–max)
1	27	15 (2–35)	1.1 (0.1– 4.7)
2	25	23 (7–57)	1.2 (0.1–12.0)
3	27	30 (12–86)	4.0 (0.7–45.6)
4	8	18 (8–28)	0.6 (0.1– 2.2)

Table 3. The species occurrence in the sampled lakes before acidification (N = number of lakes).

Species	Occurrence (N)	Occurrence (%)
Perch (*Perca fluviatilis* L.)	84	96
Roach (*Rutilus rutilus* (L.))	62	71
Northern pike (*Esox lucius* (L.))	60	69
Brown trout (*Salmo trutta* L.)	37	42
European minnow (*Phoxinus phoxinus* (L.))	33	38
Arctic char (*Salvelinus alpinus* (L.))	27	31
Burbot (*Lota lota* (L.))	26	30
Cisco (*Coregonus albula* (L.))	24	28
Whitefish (*Coregonus* spp.)	23	26
Ruffe (*Gymnocephalus cernua* (L.))	15	17
Bream (*Abramis brama* (L.))	14	16
Smelt (*Osmerus eperlanus* (L.))	10	11
Bleak (*Alburnus alburnus* (L.))	9	10
Tench (*Tinca tinca* (L.))	9	10
Rudd (*Scardinius erythrophtalmus* (L.))	5	6
Brook trout (*Salvelinus fontinalis* (M.))	5	6
Bullhead (*Cottus gobio* L.)	3	3
Alpine Bullhead (*Cottus poecilopus* L.)	2	2
Stickleback (*Gasterosteus aculeatus* L.)	2	2
Silver bream (*Blicca bjoerkna* (L.))	2	2
Pikeperch (*Stizostedion lucioperca* (L.))	1	1
Ide (*Leuciscus idus* (L.))	1	1

cantly with respect to latitude. Brown trout lakes had comparatively small areas, whereas the roach/pike lakes, whitefish/cisco lakes and Arctic char lakes had larger areas (Table 1). The Arctic char lakes were situated at the highest altitudes. These lakes also had the greatest depth and longest water retention time (Table 2). The whitefish/cisco lakes were in general situated at low altitude, and although being relatively large and deep, the water retention time in these lakes was only 1.2 year (Table 1 and 2). However, the brown trout lakes and roach/pike lakes had even shorter retention time of water, 0.6 and 1.1 year, respectively.

Occurrence of fish species

The most prevalent fish species was perch followed by roach and northern pike. Perch were found in 96 % of the lakes, whereas roach and pike occurred in 71 and 69 % of the lakes, respectively (Table 3). Brown trout, European minnow, Arctic char, burbot, cisco, and whitefish were present in 26–42 % of the lakes; whereas ruffe (*Gymnocephalus cernua* (L.)), bream (*Abramis brama* (L.)), smelt (*Osmerus eperlanus* (L.)) and bleak (*Alburnus alburnus* (L.)) occurred in only 10 to 17 % of the lakes. A total of 22 species were caught, and 12 of these were considered to be extinct in one or several lakes.

Before acidification, the whitefish/cisco lakes had an average of 6.6 species per lake; whereas Arctic char lakes, roach/pike and brown trout lakes, had 5.6, 4.0 and 2.6 species per lake, respectively. The number of species correlated positively to lake area and depth, but negatively to altitude (stepwise multiple regression, $P<0.05$, $r^2=0.50$).

Water chemistry during the acidic phase

Before liming, the roach/pike and brown trout lakes had on the average the most acidic water with pH values of 5.2 and 5.3, respectively (Table 4). The whitefish/cisco and Arctic char lakes had a mean pH of 5.6 and 5.7, respectively. The percent-

Table 4. Mean values for pH, conductivity (mS/m) and water colour (mgPt/l) in the different lake types (Table 1), before and after liming (N = number of lakes).

Lake type	N	Mean pH		Conductivity		Water colour	
		Before	After	Before	After	Before	After
1	27	5.2	6.5	6.54	6.87	45	57
2	25	5.6	6.6	6.88	7.13	25	43
3	27	5.7	6.6	3.69	4.44	14	24
4	8	5.3	6.7	4.79	5.65	44	73

Table 5. Lowest measured pH, mean value of lowest measured pH and frequency (%) of low pH values (<6.0) in each lake type (Table 1), before and after liming (N= number of lakes).

Lake type	N	Lowest pH		Mean of lowest pH		Frequency (%)	
		Before	After	Before	After	Before	After
1	27	4.2	4.3	4.6	5.9	88	7
2	25	4.3	4.8	4.9	5.7	66	5
3	27	4.1	4.7	5.1	5.9	60	6
4	8	4.5	4.6	4.6	5.9	95	11

age of low pH values was highest in the roach/pike and brown trout lakes. However, the lowest measured pH (4.1) was found in the Arctic char lakes (Table 5). Conductivity of lake water was almost twice as high in roach/pike lakes and whitefish/cisco lakes as the conductivity in the Arctic char lakes, which had a mean value of 3.69 mS/m. Water colour was relatively high (44–45 mgPt/l) in the small brown trout and roach/pike lakes, but low in the Arctic char and the whitefish/cisco lakes (14–25 mgPt/l).

Extinction of fish species

During the acidic phase most of the lakes (68 %) lost at least one species and the mean number of species decreased from 4.7 to 3.6 (Table 6). Among the different fish species, European minnow showed the greatest loss of populations. It had died out in 70 % of the lakes (23 lakes) which had had minnow populations prior to acidification (Table 7). Other species with high frequencies of extinction were brown trout, roach, and Arctic char. These species were lost in 15, 22 and 8 lakes, respectively, i.e. 30–40 % of the lakes in which they had inhabited. Whitefish, burbot, bleak, cisco, bream and ruffe were less affected by acidification, and only 13–26% of these populations were lost. Perch and pike had the lowest extinction frequencies: 2 % and 8 %, respectively.

The number of extinct species per lake correlated negatively to mean pH (linear regression, $P<0.01$, $r^2=0.30$, Fig. 2). A negative correlation to water colour was also found ($P<0.05$); whereas lake area, number of species before acidification and water retention time did not correlate significantly to the number of extinct species ($P>0.1$).

Of the four different lake types, the Arctic char lakes were most severely affected by acidification; and 85 % of these lakes had lost at least one spe-

Table 6. Mean number of species in the different lake types (Table 1) before acidification, after acidification and after liming. The significance level of the differences between periods is given for each lake type and all lakes together.

	Lake type				
	1	2	3	4	All lakes
Before acidification	4.0	6.6	5.6	2.6	4.7
	***	***	***	***	***
After acidification	2.9	5.9	3.9	1.9	3.6
	*	**	**	NS	***
After liming	3.2	6.3	4.4	2.1	4.0

*= $P<0.05$, **= $P<0.01$, ***= $P<0.001$, NS=Not Significant

Table 7. Frequency of extinction and recolonization of different fish species after acidification and liming, respectively, in the studied lakes. N=number of lakes, *=no percentage value have been calculated due to a low number of lakes (N<5).

	Occurrence before acidification	Extinction frequency		Recolonization frequency in % of extinct pop.	
Species	N	%	(N)	%	(N)
European minnow	33	70	(23)	26	(6)
Brown trout	37	40	(15)	40	(6)
Roach	62	35	(22)	36	(8)
Arctic char	27	30	(8)	0	(0)
Whitefish	23	26	(6)	50	(3)
Burbot	26	23	(6)	33	(2)
Bleak	9	22	(2)	*	(2)
Cisco	24	17	(4)	*	(2)
Bream	14	14	(2)	*	(2)
Ruffe	15	13	(2)	*	(0)
Northern pike	60	8	(5)	40	(2)
Perch	84	2	(2)	*	(1)

cies (Fig. 3). The impact was less pronounced in the other three lake types. Between 50–63 % of these lakes had lost at least one species. A comparison of the number of extinct species per lake showed a similar pattern. (Fig 4.). On the average, the loss of species per lake varied between 0.72 (whitefish/cisco lakes) and 1.70 (Arctic char lakes).

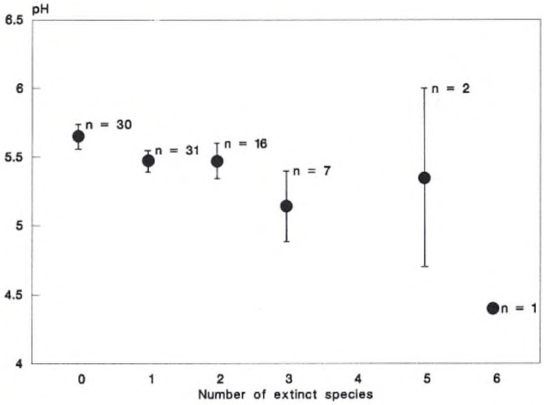

Fig. 2. Relationship between mean pH (±SE) and number of extinct species per lake (n=number of lakes).

The decrease in number of species after acidification was significant in all four lake types (paired t-test and Wilcoxon signed-ranks test (brown trout lakes), $P<0.001$). However, the extent of the decrease differed between the four lake types, even after the number of species in the original fauna was acounted for (ANCOVA, $P<0.05$ for lake type (effect) and $P<0.001$ for number of species before acidification (covariate)). The mean number of species before liming was 2.9 in the roach/pike lakes, 5.9 in the whitefish/cisco lakes, 3.9 in the Arctic char lakes, and 1.9 in the brown trout lakes (Table 6).

Recolonization of fish species

After liming, during a period of 1–18 years, many of the extinct fish species recolonized, and the mean number of species per lake increased from 3.6 to 4.0 (Table 6). The increase was significant (paired t-test and Wilcoxon signed-ranks test (brown trout lakes), $P<0.05$) in all four lake types, except for brown trout lakes. Roach recolonized 8 lakes, while minnow and brown trout recolonized 6 lakes (Table 7). The recolonization

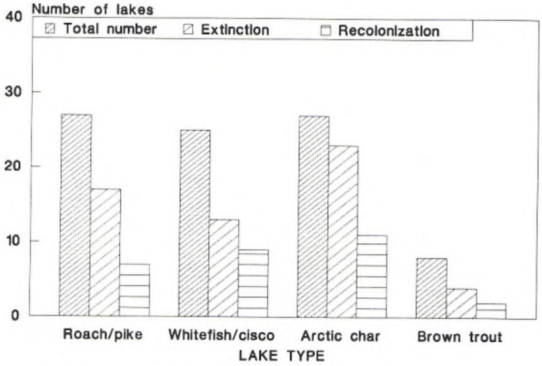

Fig. 3. Number of lakes in the different lake types with extinct and recolonized fish populations, respectively.

frequencies (recolonized populations in relation to extinct populations) varied between 26 and 50 % in these species. Whitefish, northern pike and burbot recolonized 3, 2 and 2 lakes (recolonization frequencies between 33 and 50 %), respectively. Perch, cisco, bleak and bream also recolonized some lakes, but no natural recolonization by Arctic char and the other species was recorded.

The time required for recolonization varied from 1 to 13 years, and was not significantly (Kruskal-Wallis one-way ANOVA, $P>0.24$) different between the four lake types. Furthermore, altitude, lake area, retention time of water, mean pH, conductivity and water colour did not differ significantly (Mann-Whitney U test, $P>0.14$) between lakes with and without recolonization.

Unlike the data on the extinction of species which showed significant differences between the four lake types, the increase in number of species was not significantly different between the four lake types when taking the number of species left after acidification into account (ANCOVA, $P>0.4$). Recolonization success, measured as increase in mean number of species per lake, was subsequently not significantly different between lake types. However, in per cent of total number of extinct populations the whitefish/cisco lakes had the highest frequency of recolonization (69 %), whereas Arctic char lakes, roach/pike lakes, and brown trout lakes, had lower values (40–50 %) (Fig. 5).

Diversity of the fish assemblages

In the lakes with loss of fish populations species diversity (Shannon-Wiener's index (H)) was low and did not differ between the four lakes types during the acidic phase (Kruskal-Wallis one-way ANOVA, $P>0.11$) (Fig. 6). After liming, species diversity increased significantly (Wilcoxon signed-ranks test, $P<0.05$) in the whitefish/cisco lakes, but not in the other lake types. Consequently, after liming, the species diversity differed significantly (Kruskal-Wallis one-way ANOVA, $P<0.05$) between the four lake types. Since there were no differences in the interval between lim-

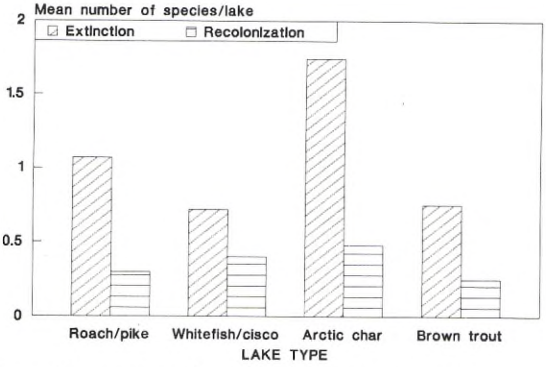

Fig. 4. The mean number of extinct and recolonized fish species per lake in the different lake types.

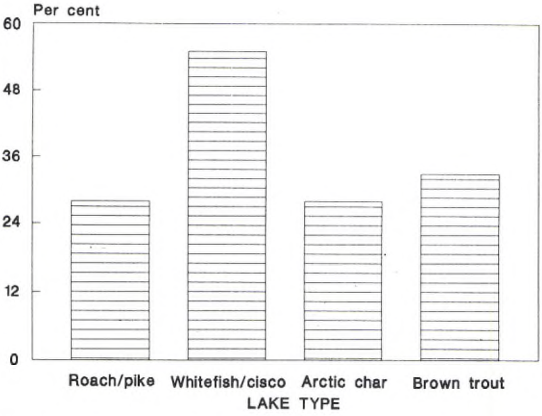

Fig. 5. Frequency of recolonization in the different lake types after liming (in per cent of extinct populations).

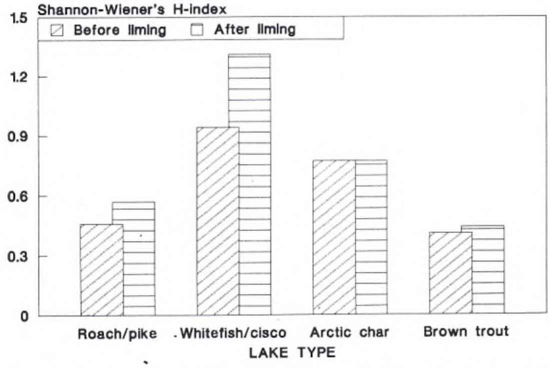

Fig. 6. Mean values of Shannon-Wiener's diversity index (H) in the different lake types, before and after liming.

ing and sampling for the different lake types (ANOVA, $P > 0.40$), this factor could not account for the differences obtained between the different lake types. The number of species and species diversity prior to liming were not significantly (Mann-Whitney U test, $P > 0.24$) different between lakes with and without recolonization.

The recolonization process and the increase in species diversity of whitefish/cisco lakes after liming may be exemplified by data from the Lake Stora Härsjön, which is classified as a whitefish/cisco lake. Roach had recolonized this lake from a lake situated upstream just 3 years after liming (Fig. 7). However an obvious increase in the abundance of roach was not noted before the abundance of cisco had increased and the abundance of perch had declined.

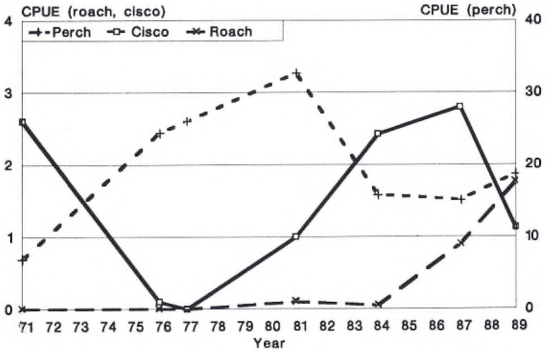

Fig. 7. Catch per unit effort (number) in the Lake Stora Härsjön after liming (1977/78).

Discussion

The percentage of lost fish populations found in the present study was somewhat higher than Almer et al. (1978) reported for a similar survey of 100 lakes located in southern Sweden. They found extinction frequencies of 43 %, 19 % and 14 % for European minnow, Arctic char and brown trout, respectively. On the other hand, the extinction percentage they reported for roach agreed with the present study. The discrepancy between the two studies may be explained by the larger number of Arctic char and brown trout lakes included in present study. In a survey of 32 Arctic char lakes in southern Sweden, Nyberg et al. (1986b) found that, due to acidification, Arctic char and brown trout had lost 30 % and 40 %, respectively, of their former populations. These extinction frequencies agree with the present findings. In comparison with extinction frequencies reported for brown trout and perch in south western Norway the population losses in this investigation are even lower. Rosseland et al. (1986) reported extinction frequencies of 30 % and 12 %, respectively, for brown trout and perch in two counties in south western Norway, during the period 1978–83. It was estimated that 71 % of the brown trout populations and 43 % of the perch populations have been lost due to acidification in these two counties by 1983.

A variety of factors influence the extinction of species in acidified lakes including: species sensitivity to acidity; water quality; lake size; geographical location; and species interactions, such as competition and predation. The most important of these factors is probably the sensitivity of each species to acidic water. Sensitivity to acidification varies between different species. European minnow, roach, Arctic char and brown trout are considered to be highly sensitive to low pH, and recruitment failure has been observed even at a pH of between 5.5 and 6.0 (Leivestad et al. 1976, Almer et al. 1978, Johansson and Milbrink 1976, Degerman and Nyberg 1989). These species were also found to be extinct in a large number of lakes in this study. Intermediate tolerance (critical values around pH 5.5) has been reported for burbot, whitefish, cisco, bleak and bream (Beamish et al.

1975, Almer et al. 1978, Leuven et al. 1987). These species also showed intermediate extinction frequencies in the present study. Perch and northern pike are considered to have high tolerance to low pH values and may tolerate pH values between 5.5 and 5.0 without reproduction failure (Almer et al. 1978, Rask 1987, Degerman and Nyberg 1989). Consequently, perch and pike were lost in only a few of the 87 lakes considered in this study.

Arctic char, brown trout and European minnow inhabit cold, oligotrophic streams and lakes, often at high altitudes, in the upper part of the water system. These streams and lakes are among the first to be acidified. Since both Arctic char and brown trout are autumn spawners, they are especially sensitive to acidification, due to the fact that the sensitive eggs and yolk-sac fry are present in the spawning grounds during late winter and early spring, when melting snow often causes sudden pH drops and increases in aluminium levels (Gunn and Keller 1986). Although minnow is not an autumn spawner it is also to high degree exposed to acid water. During their early life stages in running water both minnow and brown trout are more exposed to acid water than many other species of fish.

Roach, on the other hand, inhabit somewhat more eutrophic lakes, often at lower altitudes downstream in the water system. The occurrence of roach in acidified and limed Swedish lakes is correlated negatively to altitude, but positively to increased nutrient content of water (Degerman and Nyberg 1987). Its good competitive strength (Svärdson 1976) means that interactions with other species are less important in the extinction process than other factors. According to Svärdson (op. cit.), the population size of a species with high competitive strength, e.g. roach, whitefish and cisco, is mainly regulated by abiotic factors (e.g. pH, oxygen, nutrient level and temperature) and/or intraspecific competition. Species with low competitive strength (e.g. minnow and Arctic char) are more influenced by interspecific competition for food or predation (Svärdson 1976).

The high extinction frequencies of fish species in the Arctic char lakes indicate that this type of lakes and fish assemblages is more vulnerable to acidification than the other lake types. An Arctic char lake is often a headwater lake with a relatively small drainage area in relation to its area (Dickson et al. 1975). Acidification tends to affect Arctic char lakes more than other lakes due to characteristically high levels of precipitation and to the fact that water in these lakes has low buffering capacity. The high extinction frequencies in the Artic char lakes may therefore be related to the low concentrations of Ca^{2+} and other ions in the water (Brown 1981, Nyberg 1988). The long retention time of water prolongs further the effects of the acidic episodes during spring and autumn. The significant negative correlation between the mean pH and number of extinct species per lake indicates that the duration of the period with low pH is of great importance for extinction. Furthermore, three of the four most common fish species in the Arctic char lakes (perch, Arctic char, brown trout and European minnow) are acid sensitive species.

Although the water quality of the lakes improved after liming, the relatively low recolonization frequencies indicate that recolonization is a slow process, and that other factors, such as migration obstacles, ability to migrate, competition and predation are of great importance. The low recolonization frequencies of brown trout and minnow were probable due to a combination of factors such as insufficient liming of the tributaries to the lakes, migration obstacles, and extensive losses of populations in the water system. The low recolonization of roach is more probable to be due to migration difficulties. Other plausible factors are also a limited availability of food for fry in some of the limed lakes and predation on juvenile roach by piscivorous perch.

The likelihood of natural recolonization of Arctic char is extremely low in many cases since Arctic char tend to occur as isolated, landlocked populations (Nyman et al. 1981, Lelek 1987). In southern Sweden, Arctic char is regarded as a glacial relict and its occurrence is restricted to cold, deep, clear and oligotrophic lakes (Dickson et al. 1975, Nyberg et al. 1986b). Unfortunately such lakes are often acidified. The competitive strength of Arctic char in these lakes is low, and interactions with other fish species may limit its occurrence and the possibilities to recolonize

(Svärdson 1976, Nyberg et al. 1986b). In many cases the only way to regain Arctic char after extinction is by reintroduction (Nyberg 1988).

The high percentage of recolonization in the whitefish/cisco lakes may be related to the fact that the impact of acidification tends to be less severe in these lakes than the other lake types. Most of the whitefish/cisco lakes included in this material are situated in the lower part of the watercourses with possible sources of recolonization often located both upstream and downstream. The altitude differences between these lakes are also smaller and the probability of migration obstacles is therefore lower. Furthermore, lakes with many tributaries, such as the whitefish/cisco lakes, have a higher rate of species turnover compared to lakes without tributaries (Magnuson 1976).

Little attention has been paid to the importance of interactions between species in acidified and limed lakes. The comparison of the different lake types as to the change in diversity of the fish assemblages before and after liming indicates that the proportions among species were restored faster in the whitefish/cisco assemblages than in the other fish assemblages. One explaination for this finding is that the recolonizating species had good competitive abilities. However, although a species may have good competitive ability, other factors, such as predation can prevent recolonization or decrease the recolonization rate. In the Lake Stora Härsjön the initially slow increase in roach abundance may be due to the prevalence of predation by perch on juvenile roach. Later, when the abundance of cisco increased and abundance of perch decreased, roach could also increase in abundance.

The vulnerability to extinction of different fish species depends very much on the sensitivity of the species and its habitat to low pH, whereas the ability of a species to recolonize depends to a great degree on the distance to nearest source of possible recolonization and on the species ability to migrate. Many species are extremely limited in their abilities to migrate; whereas others, e.g. brown trout, have much greater capacities to migrate. Among non-salmonid fish, pelagic species (whitefish, cisco, smelt and pikeperch) are better adapted to swimming in running water than benthic species, such as perch, roach, ruffe and bream (Pavlov 1989). However, the abilities of both pelagic and benthic species to ascend waterfalls and cascades is about the same.

As recolonization by fish is greatly dependent on the distance to the nearest recolonization source, the extent of acid impact on the water system is of decisive importance for the recolonization rate. If a whole water system has lost most of its fish populations, natural recolonization is almost impossible. In such situations it is often necessary to reintroduce the extinct species through a fishery management programme. Although the degree of recolonization of fish species after liming is to a great extent related to physical/geographical factors, it is suggested that biotic factors such as competition and predation play an important role in the rate of successful recolonization. The above findings lead to the conclusion that the degree of recolonization of locally extinct species in a water system after liming is of vital importance for biological restoration of acidified and limed lakes. Recolonization therefore deserves more attention in the future.

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Infection of *Cystidicola farionis* Fischer (Nematoda: Spiruroidea) in the Swimbladder of Arctic Charr, *Salvelinus alpinus* (L.), from Takvatn, North Norway

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Abstract

The prevalence of infection of *Cystidicola farionis* in the swimbladder of Takvatn charr rose between age two and age five, and then stabilized at above 90 %. The intensity of infection was low up to age six, then increased sharply. These results match a life history related habitat shift by the charr. Fish, age five and older are mainly found in the littoral zone of the lake. This is also the habitat of the amphipod *Gammarus lacustris* Sars, which is the intermediate host of the parasite. The younger charr were predominantly found in the profundal and the pelagic zones where there are no *Gammarus*. Numbers of *C. farionis* often showed highly contagious distributions in the samples. Peaks in the mean intensity of infection occurred in samples from August and November and lows were seen in May and October. Charr had comparatively high rates of consumption of *Gammarus* in midsummer and probably also in late autumn. Excess mortality of heavily infected fish was indicated at winter time and during spawning when stress levels might be expected to be high. An observed increase in size of adult *C. farionis* with increasing charr age suggests that the parasite may have a long life.

Introduction

The nematode *Cystidicola farionis* is one of ten species of macroparasites found in the population of arctic charr in the oligotrophic lake Takvatn, North Norway (Heggberget et al. 1990). The third stage larva of *C. farionis* develops an infective stage in amphipods (Smith and Lankaster 1979). The only species of amphipod in Takvatn is *Gammarus lacustris*. Upon ingestion by fish, the third stage larvae migrate to the swimbladder via the pneumatic duct (Black and Lankester 1980).

The establishment of food transmitted parasites in fish depend largely on the habitat choice and the prey choice of the fish. Prior to 1985 Takvatn had a very dense population of small charr. In this high density population, the young fish were found in the profundal and the pelagic zones during the icefree season (Klemetsen et al. 1989). Profundal samples were dominated by 2+ and 3+ charr. Charr in the pelagic samples, were mostly immature and the modal age of these fish was five years (range 3–7 years).

Older charr were found along the margins of the lake, in the littoral zone. Age five fish were the youngest year class of importance in samples from this habitat. The dominant age range was 5–9 years, the modal age was seven years and many fish were mature. Because *G. lacustris*, the intermediate host of *C. farionis*, is a strictly littoral animal we expected that infection of *C. farionis* would occur in age five and older fish following the move of the charr into the littoral habitat. Svenning and Grotnes (1991) demonstrated a strong stationarity among the littoral charr in Takvatn, and Amundsen and Klemetsen (1988) found *G. lacustris* to be a regular, though not major, item in their diet. An increase in infection with age above five years was therefore also expected.

The intensities of many parasite infections have seasonal fluctuations (Kennedy 1970, Pennycuick

1971). Such fluctuations may be caused by short-term shifts in habitat and feeding by the fish (Chubb 1963, Halvorsen 1971), or by variation of the infection in the intermediate host (Awachie 1965). Charr in Takvatn had the highest intake of *G. lacustris* in July (Amundsen and Klemetsen 1988) but Amundsen (1987) also found relatively high amounts of the amphipod in charr stomachs from October 1985. July and October were therefore possible periods for high infection rates of *C. farionis*.

Mortality of the parasites within the host (Stromberg and Crites 1975), or excess mortality of the most severely infected hosts (Anderson and Gordon 1982) may cause seasonal fluctuations in the intensity of infection. Anderson (1974) argued that mass infection alone would not necessarily kill the host but weaken it to a degree where other stress factors may kill it. For charr in Takvatn the most likely times of stress are the long and cold winter and the spawning period.

The sizes of mature *C. farionis* have been shown to vary both within and between hosts (Lankester and Smith 1980). Black and Lankester (1981, 1984) demonstrated that the maximum lengths of mature females of *Cystidicola cristivomeri* White, increased with the age of the lake charr, *Salvelinus namaycush* (Walb.). They concluded that *C. cristivomeri* may live as long as 10 years in the lake charr. This is a notable exception to the general finding that adult fish parasites seldomly live longer than 1–2 years (Kennedy 1975). A similar increase in adult worms with fish age could be expected with *C. farionis* in Takvatn Arctic charr.

Material and methods

Takvatn (69°07′N, 19°05′E) is an oligotrophic, dimictic lake in the River Målselv system, Troms county, North Norway. The area of the lake is 14.2 km^2 and the elevation 214 m a.s.l. The length of the ice-free season is 24 ± 4 weeks (May/June to November/December). Arctic charr is the dominant fish species, but the lake also has a large population of three-spined stickleback, *Gasterosteus aculeatus* L. and a small population of brown trout, *Salmo trutta* L. Klemetsen et al. (1989) give a description of the lake and its biota.

Littoral samples of charr were taken once a month from July to November 1985 using gillnets of bar mesh sizes 10–26 mm. One sample, from under the ice, was taken in May with wire traps. Profundal samples were taken at about 30 m depth with gillnets of bar mesh sizes 6–16 mm (Klemetsen et al. 1990). In the field, swimbladders were conserved in 70 % ethanol and physiological saline dilution of the ethanol was carried out to prevent shrinkage of the nematodes.

In the laboratory, all nematodes were carefully removed from each swimbladder under a stereomicroscope of 6–40 X magnification and sorted into four categories; termed third stage larvae (L3), fourth stage larvae (L4), adult females and adult males (Black and Lankester 1981). All worms were counted and length-measured from line drawings made with a camera lucida. Worm lengths were measured on the drawings using a computer-graphical system which enabled each measurement to be stored for further treatment. The charr were aged by surface reading of otoliths which had been stored in ethanol and were immersed in glycerol during reading.

A total of 621 charr was examined for *C. farionis*, 302 from the littoral zone and 319 from the profundal zone. The fork length span of the total material was 6–30 cm and the age span 1–11 years. Fish ≤ 4 years dominated in the profundal material, and fish ≥ 5 years dominated in the littoral material. In all, 16,632 nematodes were sorted to category and 12,632 of these were measured for length.

Results

63 % of the examined charr swimbladders were infected with *C. farionis*. Prevalence differed greatly between fish from the two habitats, being 40 % in the profundal fish and 87 % in the littoral fish. The intensity of infection differed even more markedly; the mean number of nematodes per swimbladder was 1.5 in profundal fish and 53.9 in littoral fish.

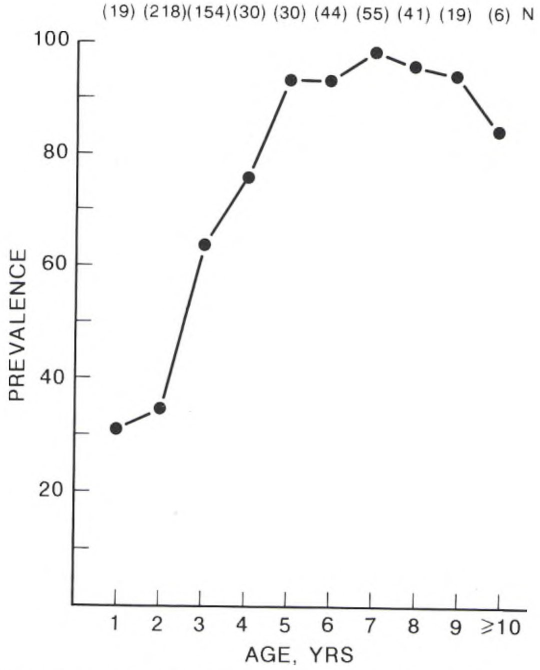

Fig. 1. Age dependent prevalence of infection (%) of *Cystidicola farionis* in benthic Takvatn charr. N: sample sizes.

Prevalence increased with fish age to age five, and then tended to stabilize (Fig. 1). As many as 31 % of the one year old fish were infected. Prevalence increased markedly from age two to age five, when 94 % of the fish were infected. For age seven charr the prevalence was 97 %. A decrease in the prevalence of infection in fish older than nine years is indicated, but the numbers of fish were too low for a definite conclusion to be drawn.

The mean intensity of infection also increased with age (Fig. 2). There was a relatively slow increase up to the age of five years, in older fish the increase was marked. In the sample of charr older than nine years the mean intensity reached 172.5 worms per fish. The most heavily infected fish carried 1,428 nematodes in the swimbladder. The increase in the intensity of infection was statistically significant between the samples of adjacent age groups two, three, four and five years old fish, and between the 2+ and 3+ samples and all older age groups (Mann-Whitney U-test, $p < 0.05$). Tests failed to demonstrate statistically significant differences between samples in older fish of different ages, but variances were very large in these samples.

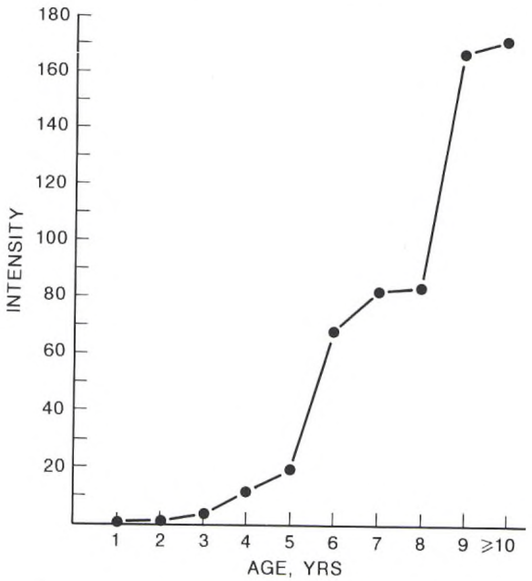

Fig. 2. Age dependent mean intensity of infection (worms per fish) of *Cystidicola farionis* in benthic Takvatn charr. Sample sizes as in Fig. 1.

The intensity of infection varied with season, increasing from 14.2 worms per fish in May to 42.2 in August. Intensity decreased in September, declined further to 14.2 in October before increasing again to 40.1 in November. The result that charr five years and older were the most heavily infected (Fig. 2), suggested that the seasonal fluctuations occurred predominantly in these age groups. There were marked differences between spawners (referring to maturing, spawning or spent fish, depending on season) and non-spawners in this respect among the five years and older fish. Among the non-spawning fish, there was a steady increase in the mean intensity of infection from 32 worms per fish in May to 143 in October (Fig. 3 A). Among the spawners, there was a sharp increase in intensity from May to August followed by a sharp decrease in September and October (Fig. 3 B). In November, there was again an increase in intensity of infection. This pattern was similar to the one described above for the total material. In general, the vari-

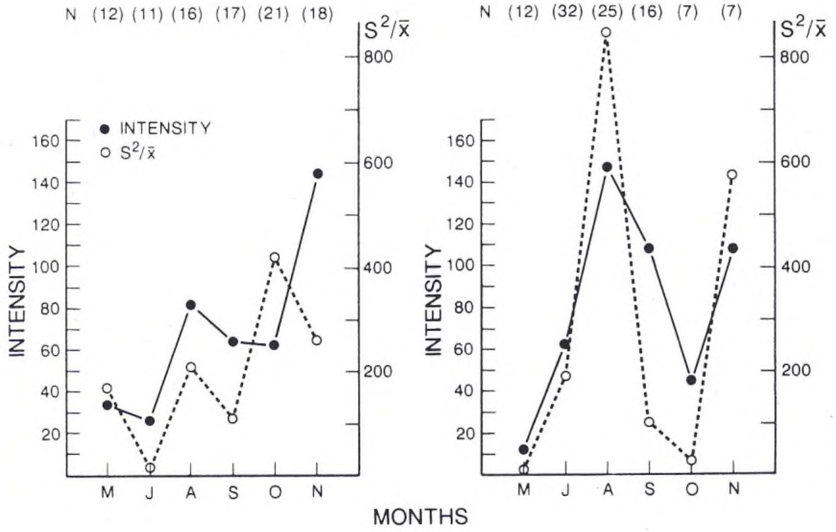

Fig. 3. Seasonal development of mean intensity of infection and variance to mean ratio of *Cystidicola farionis* in ⩾ five years old benthic Takvatn charr. Left panel (A): non-spawners; right panel (B): spawners.

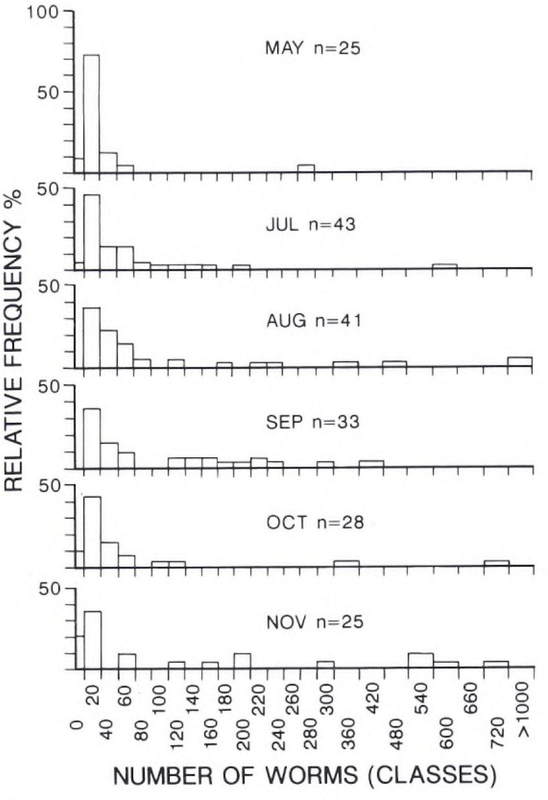

Fig. 4. Seasonal variation in the distribution of number classes of *Cystidicola farionis* in ⩾ five years old benthic Takvatn charr. Number classes are in steps of 20 worms up to 300 inclusive, and in steps of 60 worms above 300. Cases of > 1,000 worms are pooled into one class.

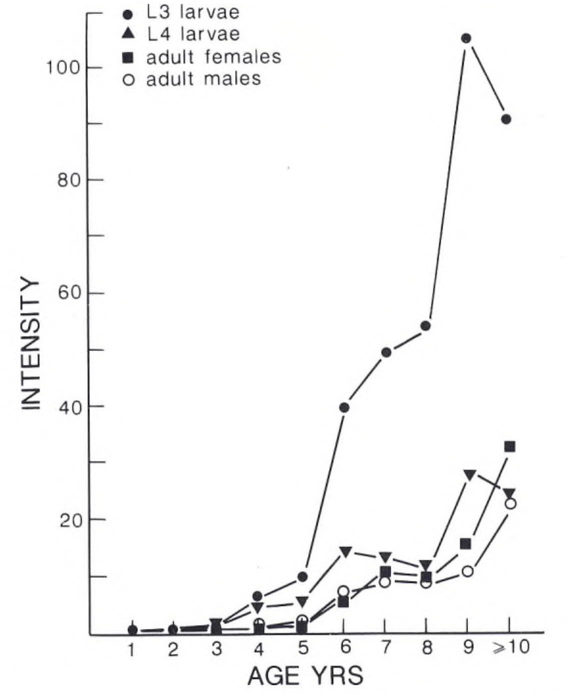

Fig. 5. Age dependent mean intensity of infection of *Cystidicola farionis* L3-larvae, L4-larvae, adult females and adult males in benthic Takvatn charr.

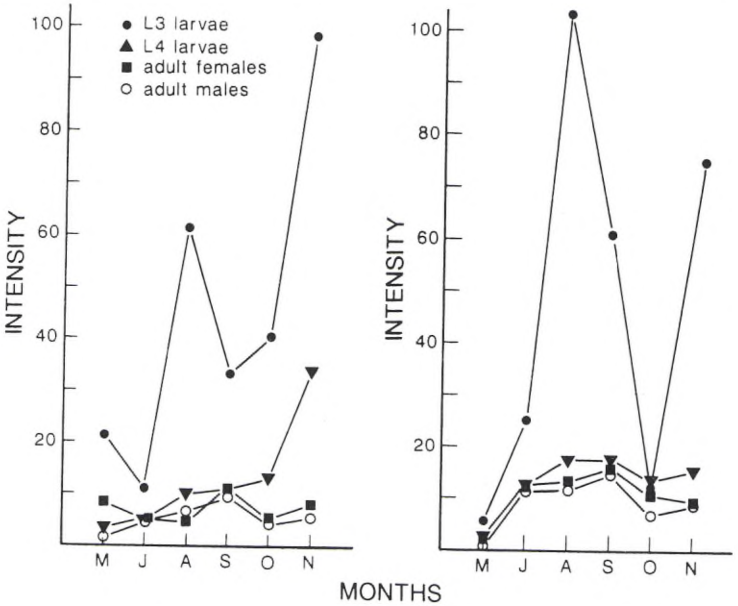

Fig. 6. Seasonal development of mean intensity of infection of *Cystidicola farionis* L3-larvae, L4-larvae, adult females and adult males in ⩾ five years old benthic Takvatn charr. Left panel (A): non-spawners; right panel (B): spawners.

ance to mean ratios followed the mean intensity patterns closely (Fig. 3 A, B). This means that the high intensity values in August, most pronounced among the spawners but also indicated in the non-spawners, and in November were caused by a number of very heavily infected fish in the samples. The opposite was the case for the spring samples for both groups (again most pronounced with the spawners) and among the spawners in October. The low mean values at these times resulted from the samples having very few fish with heavy infections.

In May, very few charr with worm numbers over 60 were present in the sample, while the August sample, in contrast, had several fish with many worms in the swimbladder. In October, relatively few fish occurred in the high number classes; while the November sample had comparatively many fish with heavy parasite burdens (Fig. 4).

The intensity of infection increased with fish age for all four categories of *C. farionis* (Fig. 5). L3-larvae increased more than the others from age three, and from age five the increase among these larvae was very strong. No adult females and males were found in the one year old charr. In fish above age six a slight preponderance of female over male worms was indicated.

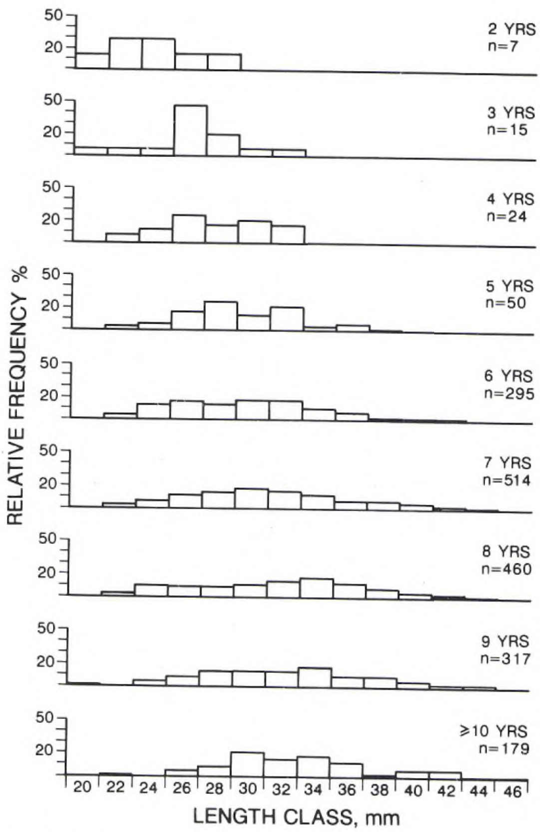

Fig. 7. Body length distributions of adult female *Cystidicola farionis* in successive year-classes of benthic Takvatn charr.

The L3 stage was the only worm category with a conspicuous seasonal variation in mean intensity of infection (Fig. 6). This variation was similar for spawners and non-spawners; with low values in May, an increase during the summer followed by a decrease in early autumn (September–October), and then a new increase in November. It follows from the results shown in Fig. 6 that the general seasonal variation in intensity of infection described above is largely the result of changes in intensity of L3-larvae.

The smallest female *C. farionis* in the material measured 20 mm, and the largest, which was found in an eleven years old charr, measured 46 mm. The mean lengths of females increased clearly with the age of the fish (Fig. 7). This increase was significant between all fish age groups (t-test, $p<0.05$).

Discussion

This study clearly demonstrated that the infection of *C. farionis* in Takvatn charr increased with the age of the fish. This has not been previously shown in Arctic charr, but Valtonen and Valtonen (1978) found that the infection of *C. farionis* in whitefish *Coregonus nasus* (Pallas) increased with the age of the fish. Lankester and Smith (1980) found that the intensity of *C. farionis* increased with increasing fish length (which was highly correlated with age) in lake whitefish *C. clupeaformis* (Mitchill), lake herring *C. artedii* Lesueur, rainbow smelt *Osmerus mordax* (Mitchill), and rainbow trout *Onchorhynchus mykiss* (Walbaum). Black and Lankester (1981, 1984) also showed that infection with the con-generic *C. cristivomeri* increased with age both in Arctic charr and in lake charr.

In Takvatn, patterns of development were different between the prevalence of infection and the intensity of infection. The prevalence increased sharply from age three while a sharp increase in the mean intensity did not become manifest before age six. The timing of the increase in intensity agreed well with the expectation that *Cystidicola* infection should build up in age five and older charr. In the high density population of Takvatn charr, the oldest and largest fish dominated in the littoral zone (Klemetsen et al. 1989). Many of these fish were sexually mature or maturing, and clearly, the adult segment of the population had occupied the ecologically most profitable habitat in the lake. The density was high, and Svenning and Grotnes (1991) were able to demonstrate a very strong stationarity and homing tendency among these fish. *Gammarus* is a highly preferred prey by salmonids; and when the Takvatn charr occurred in high densities, the amphipod population was probably cropped heavily. Nevertheless, Amundsen and Klemetsen (1988) found that *Gammarus* was a regular although never prominent item in the stomach contents of littoral charr. This combination of a high degree of stationarity and a regular occurrence of *Gammarus* in the diet of the charr in the littoral zone explain the steady increase of infection in charr after age five.

It does not, however, explain the observation that infection was seen in 1+ charr and that prevalence increased markedly in charr of three years and older. Because *G. lacustris* is a littoral species, this shows that the younger charr must have been visiting and feeding in the littoral habitat, in spite of the strong dominance of adult charr. This habitat offers the best feeding grounds in the lake, and it seems natural that young charr will occasionally try to feed there, thereby defying the intraspecific competition and also the potential predation risk they meet there. Svenning (1985) often found a proportion of small charr in beach seine hauls, especially in late autumn. It is possible that the concentration of adult fish on the spawning grounds in the autumn may create vacant littoral areas into which young, non-spawning fish can move for feeding. Klemetsen et al. (1990) found that a few age two and three charr, which were caught in the profundal zone at depths around 30 m, had eaten some littoral prey, especially in the autumn. They argued that this indicates that young, profundal charr had undertaken brief feeding trips along the bottom profile up to shallower water to take a few littoral prey. Finally, unpublished results from a winter study (R. Knudsen and F. Staldvik pers.

comm.) show that young charr reside in shallow water during the winter. There are, therefore, several ways in which infection of *Cystidicola* could occur early in the life span of the charr.

Seasonal variations in fish parasites have been discussed by several authors. Chubb (1963) concluded that the recruitment of parasites depends on the feeding habits of the fish, and Awachie (1965) found that seasonal fluctuations of *Echinorhynchus truttae* Scrank in brown trout were correlated to fluctuations in the intermediate host *Gammarus pulex* L. On the other hand, Kennedy (1970, 1975) argues that water temperature is important because it influences the behaviour of the fish and the intermediate host, the reproduction of the parasite and the development of the parasite within the intermediate host. Dahl (1917) found that *G. lacustris* had a two year life cycle in the lake Laugen in Troms, and Økland (1969) observed that it spawned in late July and early August in Sagelvvatn, close to Takvatn. Based upon findings of Black and Lankester (1981) that infection with *C. cristivomeri* was highest in the oldest specimens of the intermediate host *Mysis relicta* L., it may be inferred that the oldest *Gammarus* in Takvatn are the most heavily infected. This would be the two year old part of the population. At the reproduction time, the *Gammarus* may easily fall prey because the pairing amphipods remain together in copula for a long period. *Gammarus* occurred in the stomach contents of charr at all times during the ice-free season, but the importance was very low in June and September. In July, its mean contribution to the stomach contents was 8 % and the frequency of occurrence was 17 % (Amundsen 1984, see also Amundsen and Klemetsen 1988). The values for August and October were a little lower but still notable. More important, the daily food intake rates of the charr peaked in July and were still high in August. For a large part, this is a direct consequence of warm summer water, with the result that the charr had a comparatively high intake of *Gammarus* with potentially high infections in mid-summer. This accounts well for the observed peak of *Cystidicola* infection in August. Indirectly, this is in agreement with Kennedy's (1970, 1975) argument that temperature affects parasite fluctuations.

The late autumn peak in infection, mainly caused by third stage larvae, may also be related to feeding. Amundsen and Klemetsen (1988) found a slight increase of *Gammarus* in the charr stomachs in October. Based on a material from 1985, Amundsen (1987) found a marked peak of *Gammarus* in the stomachs in early October. He related this to a heavy storm just prior to the sampling period. At this time of the year strong winds are frequent at Takvatn and the lake is in full autumn circulation. Very likely, the mats of submerged vegetation which are dominated by the charophyte *Nitella* sp. will be torn up under such conditions, thereby exposing *Gammarus* to predation. This phenomenon which probably occurs at intervals every autumn, may give a reasonable explanation to the rise of *Cystidicola* infection in November, even though general rates of food intake are low at this time of the year (Amundsen and Klemetsen 1988).

Increased mortalities of fish parasites at high parasite densities are reported by Mills et al. (1979) and Stromberg and Crites (1975). These are, however, ecologically and systematically distant from the host-parasite relations examined in this study; and Black and Lankester (1981, 1984) pointed out that high densities of *C. cristivomeri* in *S. alpinus* and *S. namaycush* reduced the lengths of females and their reproduction rates; but found no density dependent mortality. They suggested that their results were caused by intraspecific crowding. Because *C. cristivomeri* and *C. farionis* are closely related species, we find no reason to believe that density related mortalities of the parasite were causing the seasonal troughs in the intensities of infection observed in the present case.

Crofton (1971) claimed that every parasite is capable of killing its host if it is present in high numbers. By simulation, Anderson and Gordon (1982) found that parasite induced host mortality can occur in the older year-classes of the host. Anderson (1974) concluded that huge numbers of the cestode *Caryophyllaeus laticeps* Pallas in bream *Abramis brama* L. did not kill the host directly, but weakened it to the extent that it became less resistant to environmental stress and other pathogens. During spawning, a fish undergoes great physiological stress. Much energy is shunted from the somatic tissues into the gonads, and spawning is, in itself energy consuming. Spent Takvatn charr were found to be in very poor condition, and their food intake rates were markedly below those required for activity levels (Amundsen 1984, Amundsen and Klemetsen 1988). It seems reasonable to suggest that the observed fall in the mean intensity of infection in October was caused by excess mortality of heavily infected fish after spawning. Kristoffersen (1986) put forward the same suggestion in his study of the cestodes *Diphyllobothrium dendriticum* (Nitzsch) and *D. ditremum* (Creplin) in Takvatn charr.

Winter is another possible stress period for charr in Takvatn. The lake is ice-bound for 6–7 months, and winter temperatures may be very low due to extended autumn circulation caused by continuously strong winds. Observations over several years indicate that the temperatures never exceed 2.0°C in the winter, and that values as low as 0.2°C prevail down to 15 m depth in some years. Even for the Arctic charr, such long and cold winters may inflict excess mortality in heavily infected fish, and be the reason for the low values of mean intensity of infection observed in the month of May. Kristoffersen (1986) found indications that Takvatn charr with heavy infections of *D. dendriticum* died during the winter in his study; and Henricson (1978) concluded the same for *D. dendriticum* in charr in north Sweden. There may be reason to believe that combinations of several parasites may act together to weaken the charr leading to high mortality in periods of stress.

The regular increase in body lengths of female worms with increasing fish age over many year-classes suggests that *C. farionis* may live for many years in its host in Takvatn. This result is similar to what Black and Lankester (1981) found for *C. cristivomeri* in lake charr; and indicates that the swimbladder nematodes of the genus *Cystidicola*, infecting charr species, may be an exception to the general rule that adult fish parasites have short life expectancies (Kennedy 1975).

Acknowledgments

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On Growth and Smoltification in Atlantic Salmon Parr – the Effect of Sexual Maturation and Competition

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Abstract

Competition and precocious sexual maturation are assumed to affect growth and the smoltification process of Atlantic salmon (*Salmo salar*) parr. This assumption was tested experimentally by introducing three different categories of parr (i.e. females, immature males and sexually mature males) into four different competition regimes. The parr were exposed to the regimes for five months prior to smoltification. The following parameters were analyzed and associated with the degree of competition and the category of parr: body size, specific growth rate, condition factor, cardio-somatic index, plasma 11-ketotestosterone, plasma testosterone, smolt-coloration, gill Na-K-ATPase activity, plasma chloride ion concentration and osmotic water loss. The results showed that sexually mature males had higher growth rates than other parr and were not necessarily less adapted to seawater. Competition affected the smoltification process. The plasma level of androgens was not negatively correlated with the smoltification parameter. Thus, it is not the androgen level per se, which triggers a shift in the physiological processes invoked in the smoltification process. Differences between studies, regarding the effects of androgens and sexual maturation on smoltification, may be explained by differences in environmental factors such as temperature and competition.

Introduction

Anadromous Atlantic salmon (*Salmo salar*) parr undergoe a series of complex of changes in morphology, physiology and behaviour at smoltification (Hoar 1988, for review). The age at which parr smoltify varies among populations, but recent evidence suggests that growth is a key trigger for the process of smoltification (e.g. Thorpe 1977, Thorpe and Morgan 1978, Thorpe and Wankowsky 1979). This hypothesis is based on the fact that juvenile populations develop bimodal length frequency distributions from July to November. The individuals from the upper modal group smoltify the following spring (Simpson and Thorpe 1976).

In many salmonids, males and females have adopted different life history strategies in terms of age at sexual maturation. In Atlantic salmon, males mature either as parr in freshwater, or after having spent one or several years at sea. Females usually mature only after having spent one or several years in the sea (e.g. Jones 1959).

In many populations male parr become sexually mature in the autumn prior to their smoltification the following spring (e.g. Evropeytseva 1960, Österdahl 1969, Eriksson et al. 1979). Among salmonids, the first individuals to mature are usually the fastest growers (Alm 1959). However, as a consequence of gonadal development, somatic growth should be retarded in sexually mature fish. Such mature parr predominate in the lower size modal groups (Thorpe and Morgan 1980).

Although growth seems to be an important factor involved in smolting as well as sexual maturation, the two biological states are regarded to be under physiologically incompatible processes (e.g. Evropeizeva 1960, Villarreal and Thorpe 1985, Lundqvist et al. 1988).

A number of factors have been assumed to regulate growth in Atlantic salmon parr and smolts. Under natural conditions, one may reasonably assume that inter-individual growth variation is the outcome of competition for optimal food stations. A number of experimental studies have demonstrated an association between growth and dominance in salmonids (e.g. Symons 1971, Fernö and Holm 1986, Holm and Fernö 1986, Metcalfe 1986, Davis and Olla 1987). As growth is associated with smoltification, competition may also eventually affect the smoltification process (Patiño et al. 1986).

Our objectives were (1) to determine whether sexual maturation affects smoltification and, (2) to evaluate whether competition prior to smoltification influences growth and thereby ultimately affects the smoltification process. The following parameters were analyzed: body size, specific growth rate, condition factor, cardiosomatic index, plasma 11-ketotestosterone, plasma testosterone, smolt coloration, gill Na-K-ATPase activity, plasma chloride and osmotic water loss.

Material and methods

Fish rearing procedures

The salmon parr used in the experiments were from a wild stock (River Surna, central Norway) hatched at the "Settefiskanlegg A/S", Lundamo, in the spring of 1984. Prior to the experiments, the fish were held under natural photoperiodical conditions where daylight entered through a transparent roof. Supplementary illumination was provided during working hours (8:00–16:00). On December 15, 1985, the fish were moved to the laboratory at the Department of Zoology, University of Trondheim, marked individually with Carlin tags and transferred into one of four 1 m^2 compartments in a plastic tank.

Competition is an interaction between individuals, brought about by a shared requirement for a resource in limited supply, and ultimately leading to a net loss of Darwinian fitness. Competition can take the form of exploitation or scrambled. Each individual may be affected by the amount of resources remaining after exploitation by others. Alternatively, individuals interact agonistically with each other, preventing one another from exploiting available resources in a habitat (Lomnicki 1988, Begon et al. 1990). Thus, two factors may have an impact on an individual profit from a food resource, viz., the amount of food per individual and the density of competitors. Prior to smoltification, Atlantic salmon parr can be regarded as energy maximizers. Due to their asymmetric competitive ability, each individual will not gain an equal amount of food (Järvi and Pettersen 1991). Thus, although the average amount of food per capita may be equal, the distribution of achieved individual profit will be altered when the population density changes. By varying the amount of food and the density of fish in the four compartments, the present experimental design consisted of four different regimes, where the fish were exposed to different levels of competition. Fish density was confined to 50 individuals (7.5 kg m^{-3} in May) in two compartments, and 100 individuals (15.0 kg m^{-3} in May) in the other two. The four competition regimes, ranked in order of increasing competition, were (1) 50 individuals, 150 % food ration, (2) 100 individuals, 150 % food ration, (3) 50 individuals, 75 % food ration, (4) 100 individuals, 75 % food ration. The food ration was calculated in accordance with recommendations by the manufacturer, i.e. at 0.2 % (dry food weight) of wet fish weight per day. The food used was Ewos ST-40 dry pellets with an energy content of 15.5 kJ g^{-1}. The fish were fed daily for 30 min by an automatic feeder one hour after the light had been switched on.

Each compartment was illuminated by a 15-W fluorescent, daylight tube giving 80 lux at the water surface. A natural photoperiod regime was simulated, and the cycle was adjusted once a week. A twilight period of 50 min was simulated. The water flow rate in each compartment was 3 l min^{-1}. The water temperature during the experiment was kept nearly constant at 3°C, rising to 4°C during May, the temperature at which the smolt migration is in process in central Norway (Hesthagen and Garnås 1986).

The experimental period ended on May 26, which is about the same time at which the wild parr from the River Surna strain normally smolt (Hvidsten and Mökkelgjerd 1987).

The 3.6 % mortality during the experimental period was equally distributed among the compartments and was not density dependent.

Biometric analysis

Individual weights (g) and lengths (mm) were recorded during the experiment on December 15, January 31, April 14 and May 26. The specific growth rate (G) was calculated for the total period using the formula:

$$G=(\ln(FL_2)-\ln(FL_1))*100*t^{-1}$$

where FL_2 is the total length on May 26, FL_1 is the total length on December 15, and *t* is the number of days.

Higgins (1985) suggested that physical condition, in terms of relative heart weight is correlated with smolt status. To evaluate this predictions, the fish were killed on May 26, and their hearts were dissected out (including ventricle, atrium, sinus venosus, and blood) and were weighed to the nearest 0.01 g. The relative heart weight was used as a cardio-somatic-index (CSI):

$$CSI=(HW*BW^{-1})*10^2$$

where HW is the weight of the heart and BW is the body weight in g. Such an index is sensitive to the shape of the fish body. Fat fish will have a lower CSI than slim ones of the same length. In this study Fulton's condition factor (CF) was used as an index for body shape.

$$CF=(BW_2*FL_2^{-3})*100$$

where BW_2 is the body weight (g) and FL_2 is the fork length (mm) on the May 26. Because competition was assumed to affect CF, and that there was a dependent relationship between CF and CSI, the residuals from the regression was used as cardio-somatic-index (CSI_r).

Androgen analysis

As 11-ketotestosterone (11KT) and testosterone (T) are assumed to be associated with sexual maturation (Simpson and Wright 1977, Idler et al. 1981, Hunt et al. 1982), we also included such analyses. The serum 11KT level was estimated as described by Simpson and Wright (1977), with some slight modifications. Following the extraction procedure, the extract was purified by gel chromatography, using Sephades LH-20 columns eluted with cyclohexan-ethanol-chloroform (75: 20: 10 v/v). This chromatographic method separated T and 11KT in each fraction, and also separated other interfering androgen metabolites from these fractions. The elutes were evaporated to dryness, in a nitrogen atmosphere, in a waterbath at 40°C. For the radioimmunoassay (RIA) of 11KT, the residue was dissolved in a gelatine buffer. Human plasma with three known concentrations of added 11KT was used as a control in the RIA assay. Plasma levels of T were estimated by RIA using the T fraction obtained from the chromatographic separation procedure, and human plasma with three known concentrations of T as a control. The concentration of T and 11KT was expressed as $\mu g*ml^{-1}$.

Smoltification parameters

Four different smolting criterion were used, of which one is morphological and three are physiological.

(1) Coloration, as a criteria of smolting, was estimated on May 26 according to a modification of the procedures of Johnstone and Eales (1967) and Birt and Green (1986). Each fish was classified as either unsilvered (type 0), partially silvered (types 1 and 2), or fully silvered (type 3).

(2) Gill Na-K-ATPase activity was estimated on May 26. Before sampling, the fish were starved for 24 hours. Twelve fish from each compartment were selected at random and killed with a blow on the head. Thereafter their gill apparatus was dissected out. Gill Na-K-ATPase activity was determined by a method taken from Zaugg (1982) with the following modifications: the gill filaments were frozen in liquid nitrogen; the enzyme assay was done with a 100 μl aliquot of enzyme preparation in 650 μl reaction medium (pH 7.1), and stopped after 20 min by adding H_2SO_4 (at 0°C) to obtain a final volume of 2.5 ml. Phos-

phate, hydrolysed from ATP, was determined using the method described by Fiske and Subbarow (1925). Protein in the enzyme preparation was determined by the method of Lowry et al. (1951). The enzyme activity was expressed as (μmol Pi $*$ mg^{-1} protein) $*$ h^{-1}.

(3) A sea water challenge test (24 h) was used to measure hypo-osmotic regulatory ability (Clarke and Blackburn 1977). The test was carried out in 4 m^2 tanks, with a water-level of about 45 cm, and a continuous flow of seawater. Water temperature was 10.0°C, salinity 32 ‰ and the flow rate ca 5 l $*$ min^{-1}. Four tanks were used, with 25 fish taken from each of the eight experimental compartments, i.e. a total of 50 fish in each tank. The fish were starved for 48 hours before the test and then transported a 10 min journey in oxygenated water to the test site. The test was performed about 24 hours after the fish had been anaesthetized with chlorbutanol to facilitate the weight and length measurements. The hypo-osmotic regulatory ability was estimated as the relative weight loss of the individual fish

$$WL = \ln(W_3) - \ln(W_2)$$

where W_2 is the weight on May 26 and W_3 the weight on May 27.

(4) After the seawater test, blood samples were taken from the dorsal vein with a heparinized syringe. After separation and centrifugation for 3 min by 5,000 rpm, the plasma was kept on ice for about 1 hour and then frozen at –20°C. Within 4 weeks, plasma was thawed, stirred and Cl^- measured with a Radiometer CMT Chloride titrator. The concentration of chloride ions was expressed as mmol $*$ l^{-1}.

Statistical analyses

An ANOVA procedure was performed for two way analysis of variance for factorial design. We tested the hypothesis that the means of the dependent variables were equal, for all groups. The two categorial variables were (1) categories of fish i.e. mature males (M-males), immature males (I-males) and females and (2) competition regimes ranked after increased competition (regime no. 1–4). If any significant difference was revealed by the ANOVA test procedure, a Scheffe's multiple comparison test was used in order to reveal any pairwise statistical difference in means within categories of individuals and within competition regimes, respectively. Only a significance level of 0.05 was used. When studying the associations between variables a Pearson's correlation analysis was used. Because the direction of r was predicted, one-tailed-tests were used. The two androgen parameters were $\ln(x+1)$-transformed to obtain normal distribution. The smolt coloration of the individuals was ranked and then used as a parametric data set (procedure recommended by M. J. Norusis/SPSS Inc.). The nominal values were tested for all other dependent variables. Because there was a significant covariation between CSI and CF, the residuals (CSI_r) were used after regressing CSI on CF.

Results and discussion

Somatic growth

Sex and sexual maturation

Earlier studies have revealed that the most rapidly growing males mature sexually in a cohort (e.g. Alm 1959, Leyzerovich 1973, Thorpe and Morgan 1980, Saunders et al. 1982). However, as a consequence of allocating energy to gonads and reproductive activities, the somatic growth of these males is delayed during the reproductive period. In some populations mature males are the smallest fish following reproduction (e.g. Lundqvist and Friberg 1982, Saunders et al. 1982, Kristinsson et al. 1985). When this study began in the middle of December, i.e. just after the normal spawning period for this stock, the M-males were shorter than the I-males and females (Table 1). After the spawning period, M-males will again allocate energy to somatic growth. In fact, both Kristinsson et al. (1985) and this study (Table 2) demonstrated that the M-males again adopted a relatively higher somatic growth rate than the other fish in the cohort. Due to this relatively higher growth rate, the difference in

Table 1. Analysis of differences in fork length (cm) at the beginning of the experimental period by categories of fish (CoF) (i.e. females, immature males and mature males) and competition regimes (CR).

A. Two-way ANOVA. B. Scheffe's multiple comparison test for pairwise comparisons of means.

A.

Source of Variation	DF	F	Sign. of F
Main Effects	5	5.3	0.000
CoF	2	12.7	0.000
CR	3	0.2	0.908
2-way Interactions	6	0.3	0.925
Explained	11	2.6	0.005
Residual	197		
Total	208		

B.

Categories of fish						Competition regimes						
Mean	SD	Group	F	IM	MM	Mean	SD	Group	1	2	3	4
16.2	1.8	F		—	*	15.7	1.9	1		—	—	—
15.6	1.9	IM			*	15.6	1.7	2			—	—
14.7	1.3	MM				15.9	1.4	3				—
						15.6	1.8	4				

* Denotes pairs of groups significantly different at the 0.050 level.

length between the categories of fish vanished (Table 3).

Competition

Although, competition over time conferred a density-dependent mortality on *Salmon* species (e.g. Hassell 1976, Elliott 1989), increased short term competition may result in decreased growth rate. In nature, as well as during rearing conditions, growth rate is inversely proportional to the population density when food is a limiting factor (Refstie and Kittelsen 1976, Lund and Heggberget 1985). In this study, fish living under conditions of high competition grew slower than fish living under conditions of low competition (Table 2).

Although competition may occur in the form of exploitation or interference, in salmon somatic growth is primarily affected by social dominance and access to food. In rainbow trout, (*Oncorhynchus mykiss*), a positive correlation exists between metabolic expenditure and food intake in dominant as well as subordinate fish (Metcalfe 1986). However, dominants obtain a greater intake for a given expenditure than do subordinates. This means that if subordinates adopt such a foraging strategy, they actually spend more energy than they are able to gain (Metcalfe 1986). Such a mechanism may explain why the growth of subordinate Atlantic salmon parr is significantly less than that of dominants (Symons 1971, Fernö and Holm 1986). In pairwise aggressive interactions, sexually mature parr will win more frequently over non-mature parr than vice versa (Järvi and Pettersen 1991). It is therefore reasonable to assume that it is the lower cost of social interference, which confers a higher growth rate on M-males compared to I-males and females.

Table 2. Analysis of differences in specific growth rate by categories of fish (CoF) (i.e. females, immature males and mature males) and competition regimes (CR).

A. Two-way ANOVA. B. Scheffe's multiple comparison test for pairwise comparisons of means.

A.

Source of Variation	DF	F	Sign. of F
Main Effects	5	20.9	0.000
CoF	2	30.4	0.000
CR	3	15.3	0.000
2-way Interactions	6	1.1	0.378
Explained	11	10.1	0.000
Residual	197		
Total	208		

B.

Categories of fish						Competition regimes						
Mean	SD	Group	F	IM	MM	Mean	SD	Group	1	2	3	4
0.097	0.043	F		—	*	0.136	0.052	1		—	*	*
0.107	0.069	IM			*	0.134	0.056	2			*	*
0.156	0.048	MM				0.094	0.046	3				—
						0.085	0.049	4				

* Denotes pairs of groups significantly different at the 0.050 level.

Physical condition

Although cardiac growth is largely associated with the growth of the animal, physical activity such as swimming induces increased protein synthesis in the ventricle (Houlihan et al. 1988, Farrell et al. 1988). Such an increase in the ventricular mass increases the stroke volume thereby increasing swimming ability due to higher aerobic capacity. Because the body shape (CF) covaried with CSI, the residuals CSI_r from the regression (ß=–0.15, r=–0.23, N=126, P=0.0087) were used.

A statistical analysis showed that there was a significant difference between the three categories of fish, the M-males had a significantly higher CSI_r than the females (Table 4). It is, thus, reasonable to assume that M-males are better swimmers than females. In fact, Forsman and Virtanen (1989) have revealed a better aerobic capacity during prolonged swimming for sexually mature males than for other juvenile parr. Thus, taken together, it seems evident that sexually mature parr are in better physical condition than other parr in the cohort.

Although the degree of competition did not affect the CSI_r, there was a significant interaction between categories of fish and competition regimes (Table 4). An interpretation of the interaction is that females and I-males possessed their best physical condition under a moderate ranked competition regime, while M-males possessed theirs under the highest ranking competition regime. Thus, M-males appear to be adapted to more serve competition than do the females and I-males.

Smoltification

General associations

There are several physiological changes concom-

Table 3. Analysis of differences in fork length (cm) at the end of the experimental period by categories of fish (CoF) (females, immature males and mature males) and competition regimes (CR).

A. Two-way ANOVA. B. Scheffe's multiple comparison test for pairwise comparisons of means.

A.

Source of Variation	DF	F	Sign. of F
Main Effects	5	4.0	0.002
CoF	2	2.3	0.105
CR	3	5.0	0.002
2-way Interactions	6	0.8	0.595
Explained	11	2.2	0.014
Residual	197		
Total	208		

B.

Categories of fish						Competition regimes						
Mean	SD	Group	F	IM	MM	Mean	SD	Group	1	2	3	4
17.8	1.8	F		—	—	17.9	1.8	1		—	—	*
17.4	1.9	IM			—	17.8	1.5	2			—	*
17.2	1.5	MM				17.4	1.3	3				—
						17.0	1.7	4				

* Denotes pairs of groups significantly different at the 0.050 level.

mitant with the morphological changes during smoltification. The smolts pre-adapt to seawater by increasing the Na-K-ATPase activity in the gill chloride cells. The pre-adaptation to seawater has been tested by a 24-h seawater challenge test (Parry 1960, 1961, Clarke and Blackburn 1977). In such a test, the plasma concentration of chloride ions increases and fish dehydrate (Sigholt et al. 1989). The validity of selecting a particular parameter for describing a complex biological

Table 4. Analysis of residuals of physical condition (CSI_r) after removing the effect of body shape (CF) by categories of fish (CoF) (i.e. females, immature males and mature males) and competition regimes (CR).

A. Two-way ANOVA. B. Scheffe's multiple comparison test for pairwise comparisons of means. C. Table of cell means for the two categories, CoF and CR.

A.

Source of Variation	DF	F	Sign. of F
Main Effects	5	3.7	0.004
CoF	2	6.0	0.003
CR	3	2.1	0.102
2-way Interactions	6	2.5	0.026
Explained	11	3.0	0.001
Residual	114		
Total	125		

Table 4. Cont.

B.

Categories of fish						Competition regimes						
Mean	SD	Group	F	IM	MM	Mean	SD	Group	1	2	3	4
–0.01	0.030	F		—	*	–0.01	0.025	1		—	—	—
0.00	0.046	IM			—	–0.00	0.039	2			—	—
0.02	0.039	MM				0.02	0.045	3				—
						–0.00	0.034	4				

C.

CoF/CR	1	2	3	4
F	0.00	0.00	0.01	–0.02
IM	–0.01	–0.02	0.03	0.01
MM	–0.01	0.02	0.02	0.03

* Denotes pairs of groups significantly different at the 0.050 level.

process, like smoltification, can, to some extent, be tested by correlating it with other parameter also assumed to be invoked in that particular process. However, due to the experimental set up in this study it is not possible to test all four parameters (i.e. smolt colour, gill Na-K-ATPase, plasma chloride, osmotic water loss) in an inter-correlation matrix. Smolt colour was the only parameter, which could be tested against the other smolt parameters. A Pearson's correlation ana-

Table 5. Analysis of differences in condition factor at the beginning of the experimental period by categories of fish (CoF) (females, immature males and mature males) and competition regimes (CR).

A. Two-way ANOVA. B. Scheffe's multiple comparison test for pairwise comparisons of means.

A.

Source of Variation	DF	F	Sign. of F
Main Effects	5	2.3	0.050
CoF	2	3.0	0.051
CR	3	1.6	0.179
2-way Interactions	6	0.5	0.825
Explained	11	1.3	0.235
Residual	197		
Total	208		

B.

Categories of fish						Competition regimes						
Mean	SD	Group	F	IM	MM	Mean	SD	Group	1	2	3	4
0.91	0.06	F		—	*	0.90	0.06	1		—	—	—
0.94	0.26	IM			—	0.95	0.21	2			—	—
0.98	0.08	MM				0.91	0.08	3				—
						0.92	0.06	4				

* Denotes pairs of groups significantly different at the 0.050 level.

Table 6. Analysis of differences in condition factor at the end of the experimental period by categories of fish (CoF) (i.e. females, immature males and mature males) and competition regimes (CR).

A. Two-way ANOVA. B. Scheffe's multiple comparison test for pairwise comparisons of means.

A.

Source of Variation	DF	F	Sign. of F
Main Effects	5	5.4	0.000
CoF	2	2.5	0.082
CR	3	7.6	0.000
2-way Interactions	6	0.6	0.744
Explained	11	2.8	0.002
Residual	197		
Total	208		

B.

Categories of fish						Competition regimes						
Mean	SD	Group	F	IM	MM	Mean	SD	Group	1	2	3	4
0.85	0.06	F		—	—	0.86	0.06	1		—	—	*
0.83	0.06	IM			—	0.86	0.06	2			—	*
0.85	0.07	MM				0.83	0.07	3				—
						0.82	0.06	4				

* Denotes pairs of groups significantly different at the 0.050 level.

lysis revealed that smolt colour was, as predicted, positively correlated with Na-K-ATPase activity ($r=0.22$, $N=72$, $P=0.029$), but not with osmotic water loss ($r=0.09$, $N=42$, $P=0.28$) nor, negatively, with plasma chloride ion concentration ($r=-0.23$, $N=42$, $P=0.075$). The reason for this lack of correlation between smolt colour and the other two smoltification parameters is probably due to low variation in colour among smolts. In fact, 82 % of the parr were fully silvered. Further-

Table 7. Analysis of smolt-coloration by categories of fish (Cof) (females, immature males and mature males) and competition regimes (CR). The fish are ranked according to increasing colour codes.

A. Two-way ANOVA. B. Scheffe's multiple comparison test for pairwise comparisons of means.

A.

Source of Variation	DF	F	Sign. of F
Main Effects	5	1.6	0.156
CoF	2	0.2	0.814
CR	3	2.4	0.073
2-way Interactions	6	0.7	0.685
Explained	11	1.1	0.368
Residual	197		
Total	208		

Table 7. Cont.

B.

Categories of fish						Competition regimes						
Mean	SD	Group	F	IM	MM	Mean	SD	Group	1	2	3	4
147.21	56.36	F		—	—	145.23	59.29	1		—	—	—
149.89	56.61	IM			—	137.43	63.18	2			—	—
139.64	63.70	MM				169.89	24.34	3				—
						141.61	67.72	4				

* Denotes pairs of groups significantly different at the 0.050 level.

Table 8. Analysis of Na-K-ATPase activity by categories of fish (CoF) (i.e. females, immature males and mature males) and competition regimes (CR).

A. Two-way ANOVA. B. Scheffe's multiple comparison test for pairwise comparisons of means.

A.

Source of Variation	DF	F	Sign. of F
Main Effects	5	6.3	0.000
CoF	2	1.9	0.158
CR	3	9.9	0.000
2-way Interactions	6	1.6	0.167
Explained	11	3.7	0.000
Residual	60		
Total	71		

B.

Categories of fish						Competition regimes						
Mean	SD	Group	F	IM	MM	Mean	SD	Group	1	2	3	4
6.24	1.62	F		—	—	6.53	1.07	1		—	—	*
6.15	1.70	IM			—	7.22	1.32	2			—	*
6.74	1.68	MM				6.48	1.95	3				—
						5.06	1.39	4				

* Denotes pairs of groups significantly different at the 0.050 level.

more, the osmotic water loss was negatively correlated with the concentration of chloride ions in the blood ($r=-0.50$, $N=42$, $P=0.000$).

Sexual maturation

A number of studies have shown that precocious sexual maturation may result in delayed smoltification, reduced growth and increased mortality (e.g. Dalley et al. 1983, Myers 1984, Myers et al. 1986, Lundqvist et al. 1988). The differential allocation of energy into gonads instead of soma, results in a higher condition factor for sexually mature males than for the other parr in the cohort (Saunders et al. 1982). In this study, the M-males had a significantly higher CF than the females

Table 9. Analysis of chloride ion concentration by categories of fish (CoF) (i.e. females, immature males and mature males) and competition regimes (CR).

A. Two-way ANOVA. B. Scheffe's multiple comparison test for pairwise comparisons of means.

A.

Source of Variation	DF	F	Sign. of F
Main Effects	5	1.7	0.177
CoF	2	0.1	0.911
CR	3	2.2	0.106
2-way Interactions	5	1.2	0.346
Explained	10	1.4	0.223
Residual	29		
Total	39		

B.

Categories of fish						Competition regimes						
Mean	SD	Group	F	IM	MM	Mean	SD	Group	1	2	3	4
151	20	F		—	—	166	34	1		—	—	—
160	25	IM			—	148	5	2			—	—
160	26	MM			—	148	12	3				—
						170	25	4				

* Denotes pairs of groups significantly different at the 0.050 level.

(Table 5). However, in May, the significant difference in mean CF between the females and the M-males has disappeared (Table 6). Parr have characteristic parr markings, are brightly coloured and blend with their background in a cryptic fashion (Jones 1959). In contrast, smolts are conspicuously silvery and have a black margin on the caudal fin (Johnstone and Eales 1968). In this study, there was no significant difference in coloration between the three categories of fish, viz. M-males, I-males and females (Table 7). Neither were there any statistical differences between the three categories of fish for any other of the physiological parameters including gill Na-K-ATPase activity (Table 8), plasma chloride ion concentration (Table 9) and osmotic water loss (Table 10).

Competition

An energetic deficiency can act on at least two levels. Firstly, it seems that critical size and/or growth rate are important factors in the timing of smoltification (Thorpe 1977, Thorpe and Morgen 1978, Thorpe and Wankowsky 1979). Body size and growth are associated with a fish's competitive ability and the degree of competition (e.g. Holm and Fernö 1986, Metcalfe 1986). Secondly, there is an energetic cost involved in the parr-smolt transformation. This cost is indicated by increased O_2 consumption (Maxime et al. 1989), greater respiratory enzyme activity (Blake et al. 1984) and increased thyroid hormone levels (Hoar 1976). During smoltification, increased metabolic activities invoke a mobilization of energy reserves in parr (e.g. Wendt and Saunders 1973, Virtanen 1987). Thus, intense competition during that time should entail a reduced capacity for parr to smoltify. In fact, long term studies on coho salmon (*O. kisutch*) have shown that smoltification, in terms of lowered plasma thyroid hormone levels and decreased Na-K-ATPase activity, is negatively affected by increasing population den-

Table 10. Analysis of osmotic waterloss by categories of fish (CoF) (i.e. females, immature males and mature males) and competition regimes (CR).

A. Two-way ANOVA. B. Scheffe's multiple comparison test for pairwise comparisons of means.

A.

Source of Variation	DF	F	Sign. of F
Main Effects	5	1.022	0.423
CoF	2	0.465	0.633
CR	3	0.917	0.445
2-way Interactions	5	0.484	0.786
Explained	10	0.753	0.671
Residual	29		
Total	39		

B.

Categories of fish						Competition regimes						
Mean	SD	Group	F	IM	MM	Mean	SD	Group	1	2	3	4
–0.023	0.119	F		—	—	–0.072	0.060	1		—	—	—
–0.067	0.049	IM			—	–0.021	0.129	2			—	—
–0.061	0.044	MM				–0.036	0.023	3				—
						–0.095	0.045	4				

* Denotes pairs of groups significantly different at the 0.050 level.

sity (Patiño et al. 1986). The results from this study showed that parr, living under assumedly more intense level of competition, had lower Na-K-ATPase activity (Table 8), but there were no significant differences in mean smolt coloration (Table 7), mean chloride ion concentration (Table 9) or mean osmotic water loss (Table 10) between the four different competition regimes. Based on our findings that mean Na-K-ATPase activity is negatively associated with increasing competition, it is reasonable to suggest that smoltification may be strongly influenced by the degree of competition.

Interaction between sexual maturation and competition

One factor which should reduce the ability of the M-males to smoltify is based on an assumed, increased, energetic cost for their metamorphosis compared to non-mature parr. Thus, during severe competition, one should expect that smoltification may be delayed or inhibited in sexually mature males relative to immature parr. This assumption could not be verified in the present laboratory experiment, because there was no significant interaction between the categories of fish and competition regimes, regarding smolt colour (Table 7), Na-K-ATPase activity (Table 8), plasma chloride ion concentration (Table 9) or osmotic water loss (Table 10). Thus, the energetic cost of smoltification of M-males may not be significantly higher than for other parr.

Androgens and smoltification

Plasma levels of the androgens testosterone (T) and 11-ketotestosterone (11KT) are high in maturing males before spawning (Simpson and Wright 1977, Idler et al. 1981, Hunt et al. 1982). These androgens are reported to be low at the onset of smoltification in amago salmon (*O. rhodurus*)

Table 11. Analysis of level of ll-ketotestosterone in blood by categories of fish (CoF) (i.e. females, immature males and mature males) and competition regimes (CR).

A. Two-way ANOVA. B. Scheffe's multiple comparison test for pairwise comparisons of means.

A.

Source of Variation	DF	F	Sign. of F
Main Effects	5	4.4	0.003
CoF	2	3.7	0.034
CR	3	5.1	0.005
2-way Interactions	6	1.8	0.124
Explained	11	3.0	0.007
Residual	35		
Total	46		

B.

Categories of fish						Competition regimes						
Mean	SD	Group	F	IM	MM	Mean	SD	Group	1	2	3	4
2.205	2.164	F		—	—	3.524	1.991	1		—	—	—
3.594	2.218	IM			—	3.399	2.882	2			—	—
3.989	2.609	MM				4.976	0.806	3				*
						1.759	2.032	4				

* Denotes pairs of groups significantly different at the 0.050 level.

(Nagahama 1985). In this study, there was a significant difference in mean 11KT between the three categories of fish (Table 11). No such difference was found in mean plasma T (Table 12). The reported impaired adaptation to seawater in sexually mature parr has been suggested to be inhibited by T and 11KT (Lundqvist et al. 1989). This hypothesis is supported by the fact that implantation of gonadal androgens seemingly impaired seawater adaptation in both sexually mature males and immature parr (Lundqvist et al. 1989). An obvious prediction from this hypothesis is that there should be a negative correlation between androgen level and seawater adaptation. No such correlation was found between 11KT, T and smolt colour, or between 11KT, T and Na-K-ATPase activity (Table 13). Thus, it seems that androgens per se do not impair smoltification.

There was a significant difference in mean 11KT between the four competition regimes, and the fish exposed to the highest degree of competition had the lowest androgen levels (Table 11). Such a difference may be due to that competition initiates gonadal regression. In fact, there are a number of studies on fish showing that the two main competition factors, food availability and stress, may initiate gonadal regression (Lamm 1983; for review). However, this picture is complicated by the fact that gonadal steroids have an anabolic effect and, hence, are invoked in somatic growth. In this study growth was positively correlated with both T and 11KT (Table 13).

Association between body size and smoltification

In general, larger smolts of immature fish and precociously mature males have a significantly higher rate of recapture than small smolts (e.g. Carlin 1955, Isaksson and Bergman 1978, Lundqvist et al. 1988). The fact that larger smolts seem

Table 12. Analysis of blood testosterone by categories of fish (CoF) (i.e. females, immature males and mature males) and competition regimes (CR).

A. Two-way ANOVA. B. Scheffe's multiple comparison test for pairwise comparisons of means.

A.

Source of Variation	DF	F	Sign. of F
Main Effects	5	1.1	0.385
CoF	2	0.5	0.586
CR	3	1.7	0.185
2-way Interactions	6	1.1	0.378
Explained	11	1.1	0.392
Residual	35		
Total	46		

B.

Categories of fish					
Mean	SD	Group	F	IM	MM
3.304	2.161	F		—	—
3.038	1.987	IM			—
2.936	2.003	MM			

Competition regimes						
Mean	SD	Group	1	2	3	4
3.663	1.505	1		—	—	—
2.842	2.528	2			—	—
3.526	1.471	3				—
2.485	2.049	4				

* Denotes pairs of groups significantly different at the 0.050 level.

to survive better might be due to size dependent predation (Lundqvist et al. 1988). Another explanation is that larger smolts are 'better smolts', in terms of a better seawater adaptability, due to their smaller volume/body mass relationship. In seawater, osmotic stress will inhibit the normal anti-predatory behaviour of the smolt (Järvi 1989a). Hence, larger smolts should survive relatively better. In this study, larger smolts were less exposed to osmotic stress, expressed as osmotic water loss (Table 14). There was, furthermore, also a correlation between fork length and

Table 13. The correlation between smoltification parameters, body size, condition factor, specific growth rate and androgens (11-ketotestosterone and testosterone).

	11-ketotestosterone			testosterone		
	r	N	P	r	N	P
Smoltification						
Smolt colour	0.04	48	0.39	0.20	48	0.086
Na-K-ATPase	–0.04	30	0.42	0.26	30	0.085
Body size						
Fork length	–0.18	48	0.11	0.01	48	0.47
Condition factor	0.11	48	0.24	0.12	48	0.22
Growth rate	0.25	48	0.04	0.26	48	0.04

Table 14. Association between fork length, condition factor (CF), specific growth rate (SGR), physical condition and smoltification parameters.

	Smolt colour			ATPase			Chloride ion			Water loss		
	r	N	P	r	N	P	r	N	P	r	N	P
Fork length	0.15	293	0.004	–0.15	71	0.11	0.04	42	0.39	–0.33	42	0.015
CF	–0.22	293	0.000	–0.08	71	0.26	0.02	42	0.44	0.06	42	0.34
SGR	–0.03	293	0.31	0.38	71	0.001	–0.17	42	–0.17	0.91	42	0.28
CSI_r	0.04	126	0.31	0.12	71	0.16	—	—	—	—	—	—

smolt colour, and a negative correlation between CF and smolt colour (Table 14). Thus, small body size may per se confer a higher degree of osmotic stress on the smolts. Furthermore, we found that specific growth rate prior to smoltification was positively associated with one of the physiological processes invoked in smoltification, viz., gill Na-K-ATPase activity (Table 14).

One factor, which ultimately confers a selection pressure on the smolts, is their ability to escape from predators. Larger smolts have a better ability to escape predators, as they exhibit higher swimming stamina. Thus, there is selective pressure on body size. In seawater, osmotic stress may reduce smolt ability to escape predators (Järvi 1989 a, 1990). Osmotic stress and stress caused by the presence of predators, may also cause the death of the smolts (Järvi 1989b). Thus, although anadromy in salmon is a rather old phenomenon in evolutionary terms, there is still high selective pressure on the proximate mechanisms invoked in the smoltification process.

Conclusion

This study has basically demonstrated three factors:

(1) Sexually mature parr have higher viability than other parr. This is based on the following facts: M-males have (i) higher growth rate in fresh water (Kristinsson et al. 1985, this study) as well as in seawater (Skilbrei 1990), (ii) relatively larger hearts (this study), (iii) better swimming performance (Forsman and Virtanen 1989), (iv) better competitive ability (Järvi and Pettersen 1991), and (v) lower prevalence of fin erosion (Mork et al. 1989).

(2) Sexually mature parr, are not obligatorily less adapted to seawater as smolts than other smolts (this study).

(3) Thus, from (1) and (2) it seems to be a paradox that M-males, as smolt, in some cases can be exposed to higher mortality than other smolts, not only due to impaired seawater adaptation, but also due to increased predation (e.g. Lundqvist et al. 1988). However, salmon are poikilothermic, temperature as well as competition are two important factors regulating both the gonadal regression and the smoltification process in the rivers and, thus, those two factors will ultimately have a significant impact on the survival of smolts in the sea.

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Resource Sharing in Atlantic Salmon: A Test of Different Distribution Models on Sexually Mature and Immature Parr

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Abstract

Cardinal dominance rank studies, made under experimental conditions, showed that sexually mature Atlantic salmon parr dominate over immature parr during the spring prior smoltification. Salmon parr are supposed to compete for feeding patches in nature. Hence, mature and immature parr were supposed to distribute themselves between food patches according to the following alternative hypotheses. 1) The two categories of parr should distribute themselves at random between food patches; 2) The two categories of parr should distribute themselves according to an ideal free distribution; 3) The two categories of parr should distribute themselves according to an ideal despotic distribution. In a two-patch choice experiment, we tested the predictions from the three distribution models on a mixed population of mature and immature parr. Series of experiments revealed that a random distribution model could be rejected due to an over usage, and that an ideal free distribution model and an ideal despotic distribution model could be rejected due to an under usage of the resources in the good patch. The divergence from the predictions is probably due to a tendency among some of the mature parr to occupy the good patch. Hence, the other parr were then not able to approach this patch to an extent predicted from the theories of ideal free distribution and ideal despotic distribution. In addition some perceptual constraints may be operative on the individuals resulting in an under-usage of the good patch.

Introduction

Juvenile Atlantic salmon, *Salmo salar*, primarily occupy feeding stations in streams from which they intercept their drifting prey (e.g. Wankowski and Thorpe 1979). The feeding stations (patches) differ in profitability and each individual faces a decision concerning the choice of food patch.

When resources are patchily distributed and the patches vary in value, natural selection will favours those individuals which feed in the patches in which they can maximize their net energy gain (e.g. MacArthur and Pianka 1966, Schoener 1971). A number of models have been developed to explain how competing individuals should distribute themselves in order to attain that objective.

Fretwell and Lucas (1970) introduced the theory of the ideal free distribution (IFD), in which the stable situation (i.e. an evolutionary stable strategy) occurs when all animals in a population are able to achieve the same gain, i.e. when the frequency of individuals in a patch equals the relative value of the patch (e.g. Fretwell 1972, Milinski 1979). The IFD theory assumes that animals have a perfect knowledge of their environment, have unimpeded access to all feeding patches, and have equal needs and competitive ability. In addition, the patches are considered to be homogeneous with respect to the features relevant to survival, and the suitability of a patch decreases with increasing density of individuals (Milinski 1984, Houston and McNamara 1988).

In nature, however, the competitive abilities of individuals are seldom equal. Fretwell (1972) has therefore suggested an ideal despotic distribution (IDD) model. Sutherland and Parker (1985) and Parker and Sutherland (1986) extended this to show that an ESS is obtained when the individuals are so distributed that the sum of their competitive abilities in a patch is equal to the relative value of the patch. However, several ESS solutions may occur. Houston and McNamara (1988) therefore incorporated statistical mechanics to find the most probable solution.

Although, the underlying principle for a true IFD is violated by the existence of differences in competitive ability, the individuals could in fact distribute themselves according to such a distribution if a relative pay-off-sum learning rule is operative (Milinski 1984, Regelman 1984). Harley (1981) proposed that the relative pay-off-sum learning rule, when adopted by a population, cannot be invaded by a mutant with a different learning rule. The basic principle is that each individual calculates the probabilities of visiting each patch according to the ratio of the profitabilities which the individual themselves has measured before, via its own food intake, and stored in memory. If such a rule should be operative the following assumptions must be fully satisfied. The parr must have a low memory of the two patches when the experiment starts. Each individual measures only its own feeding success. Each individual has a memory which decreases exponentially with time (see Harley (1981), Milinski (1984), Regelman (1984) for further information about the principle).

The foraging tactics of juvenile Atlantic salmon vary in relation to both biotic and abiotic factors (Wankowski and Thorpe 1979). The parr adapt their social behaviour to the stream velocity. In situations with high current velocity parr defended feeding patches, in contrast to the shoaling behaviour shown in low current velocity situations (e.g. Kalleberg 1958). A shoal type social structure was also shown by large-sized parr, although a dominance rank order was maintained within a shoal (Wankowski and Thorpe 1979).

In the autumn before they make their seaward migration, some of the male parr become sexually mature. Circumstantial evidence suggests that the dominant parr are those that mature sexually. The mature parr grow faster (e.g. Alm 1959, Thorpe et al. 1983), but because they allocate their energy resources into gonad formation, their somatic growth is reduced and eventually they become the smallest parr in the cohort. After the spawning period, however, the mature parr grow faster than the other once more and at the time of the seaward migration, or during their first year in the sea, the mature parr become as large as the other individuals (Thorpe and Morgan 1980, Skilbrei 1990, Järvi et al. 1991). Thus, it seems reasonable to suggest that the sexually mature parr will dominate over the other parr and are thereby able, on average, to profit more from the available food resources.

How then should mature parr and immature parr distribute themselves between food patches in order to maximize their net energy gain during the spring prior to smoltification? Since the assumption of equal competitive ability is violated, they should not act according to the IFD. However, by simulating a model that invoked the relative pay-off-sum learning rule, Regelman (1984) was able to show that individuals with differing competitive abilities should, in fact, distribute themselves according to a true IFD. Thus, either the IDD-model or the IFD-model could be operative.

The aim of our research was to investigate whether mature parr are de facto dominant over immature parr and, if so, whether the parr distribute themselves between food patches according to Regelman's rule, by mimicking a true ideal free distribution, or according to ideal despotic distribution or according to the H_0 hypothesis, i.e. at random.

Material and methods

Competitive ability experiments

Experimental fish

On the 30th and 31st of January 1989 (i.e. after the spawning period), 200 mature and 200 immature two-year-old parr were sampled from an ordinary rearing tank at the Research Station for Freshwater Fish at Ims (southwestern Norway). The fish originated from the River Bondal. The mature males were recognized by their ripe milt. The mature parr were then marked with two

Table 1. The average total lengths and body weights of the mature (M) and immature parr (IM), sampled from the fish population used in this study.

		Total length (mm)				Body weight (g)			
	N	Mean	SD	t	P	Mean	SD	t	P
M	40	256	22.2	−4.1	<0.01	177	50.2	−5.1	<0.001
IM	40	276	20.8			226	45.3		

yellow pearls, and the immature with two blue pearls. After being marked, the parr were kept in a 7 m^2 tank for 16 days before the behaviourial studies started. The average body size is shown in Table 1. The fish were not fed during the observation period and each fish was used only once.

Experimental design

Dominance rank and competitive ability can be regarded as analogous concepts since both are related to the probability of gaining access to limited food resources. By using the method of assigning a cardinal dominance rank, it is possible to assess the relative ranking of any two individuals (see Boyd and Silk (1983) for further details). From the storage tank, two mature and two immature parr were taken and placed in a study tank (the arena) in each trial (Fig. 1). Their behaviour was recorded on video tape for three hours, for later analysis. During the behaviourial analyses, the winner and the loser of each pairwise interaction were entered in an interaction matrix. A parr noted as a 'looser' was either chased away or had responded with withdrawal from an agonistic interaction. A more detailed description of the agonistic behaviour of the salmon parr is given by Kalleberg (1958). Within each trial, the probability of any individual winning a confrontation (P_i) with any other individual was calculated, using Boyd and Silk's (1983) method for analyzing cardinal ranks. A total of 12 trials were conducted.

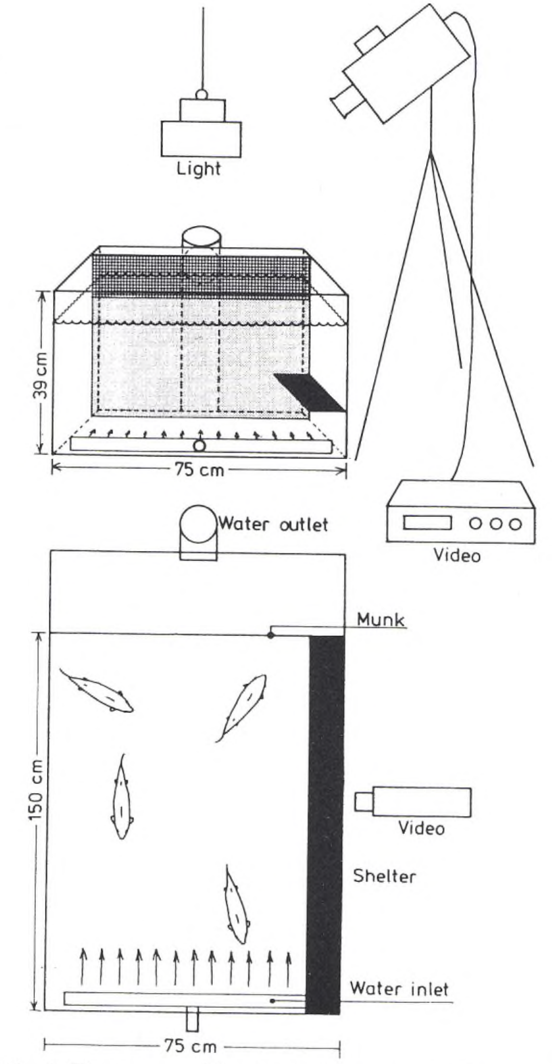

Fig. 1. The arena used for the dominance study. The water inlet was a 50 cm long pipe with holes (3 mm diam.) at 5 cm intervals. The water outlet was a munk controlling a maximum water level of 22.5 cm. The water flow was 12 l·min^{-1} The water temperature varied between 4.0 to 4.9°C. A video camera was placed over the arena. Two Thorn Polylux 36 W were placed 80 cm above the tank.

Resource sharing experiments

Experimental fish

A total of 72 mature parr and 144 immature parr

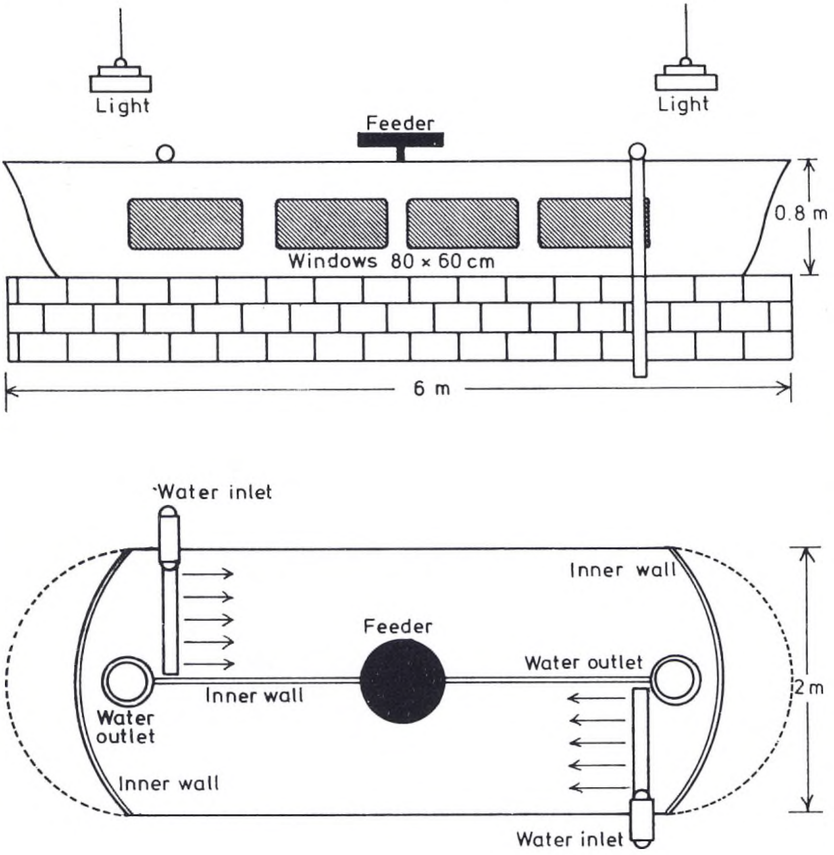

Fig. 2. The arena used for the patch choice experiments. A 10–15 cm thick layer of gravel was placed on the bottom. The gravel varied in grade size (4 to 10 cm diam.). The water inlet was placed on the gravel surface, the water velocity, 2 m behind the inlet, was 0.1 $m \cdot s^{-1}$ on both the bottom and in the overlying water body. To reduce the size of the non-profitable area, internal partitions were inserted at both ends. A circular feeder (50 cm diam.) was placed in the middle of the arena. The feeder supplied food on both sides simultaneously, giving two food patches separated by the internal wall. The feeder was controlled from a programable timer (Alma MKII).

was sampled from the same rearing tank as the fish used in the dominance study. Each fish was only used once.

Experimental design

To find out, empirically, how mature and immature parr distribute themselves between two food patches of different resource value, a patch choice experiment was conducted during the period 14th of March to 8th of April 1989. The experiments were made in two, identical tanks (Fig. 2). A choice between two food patches was offered to the fish; one good with 80 % of the available food supply (4 pellets/40 min.), and one bad, with only 20 % (1 pellet/40 min.). The food offered was Ewos pellets, no. 4 size. The amount of the food supplied was only half of what is recommended by Ewos for a similar number of individuals of that size and with a water temperature of 4–5°C.

On day 0, the fish were placed in the aquarium between 10:00 and 12:00 a.m. On the same day, at 5:00 p.m., the feeder was filled. On day 1, at 9:00 a.m., the observations were started, by noting the number of mature and immature parr in the good and the bad sides of the tank, respectively. Observations were made at 9:00 a.m., 1:00 p.m., 5:00 p.m., 9:00 p.m. each day. The feeder was re-filled at 5:00 p.m. each day. Each trial lasted for four days and, thus, 16 observations were noted from each trial. A total of eight trials were made. To obviate systematical errors, the good patch was switched on the right-hand side of the tank on four occasions and on the left-hand side on four occasions.

Table 2. The average probability for winning an agonistic pair-wise interaction for two mature (M1, M2) and two immature parr (IM1, IM2) for all 12 trials taken together. The mature parr scoring the highest probability was M1, followed by M2, and the highest scoring immature parr was IM1 followed by IM2.

		Winner			
		M1	M2	IM1	IM2
Loser	M1	—	0.44	0.39	0.21
	M2	0.56	—	0.45	0.31
	IM1	0.61	0.55	—	0.42
	IM2	0.79	0.69	0.58	—

Results

Competitive ability experiment

The probability for a given parr to win over another parr (P_i) was calculated from the interaction matrices by using the method of cardinal rank ordination (Table 2). The median P_i was significantly higher for the mature parr than for the immature parr (Wilcoxon rank test: $Z=2.02$, $P<0.05$) (Fig. 3). Hence, mature parr clearly possessed a greater competitive ability than the immature parr.

Resource sharing experiment

Hypotheses

The following three hypothesis were tested:

- H_o The parr distribute themselves at random between the two resources;
- H_1 Applying to Regelmans's rule the parr distribute themselves according to IFD;
- H_2 The parr distribute themselves according to IDD.

The predictions from the H_o and H_1 hypotheses are easy to calculate. A random distribution implies that, on average, 50 % of the parr should be found in the good patch. Because 80 % of the total food resource was located in the good patch, the IFD predictions is that 80 % of the parr should be found in the good patch. To make a quantitative test of the IDD theory, a simulation was done, based on Houston and McNamara's (1988) model. The IDD is stable when

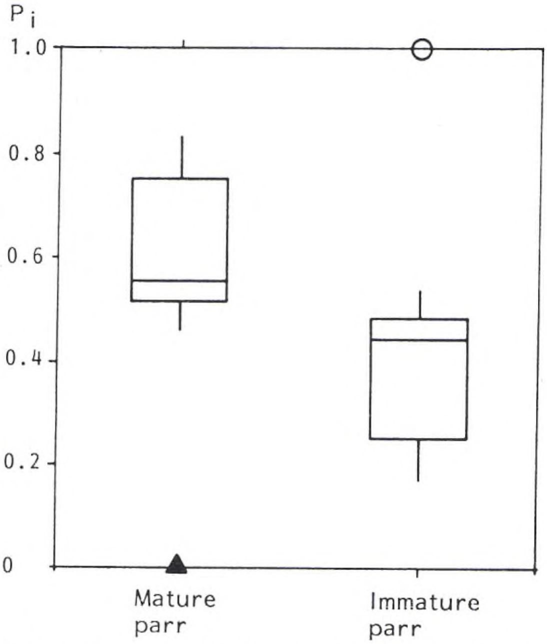

Fig. 3. A Box- and -Whisker plot showing the probability (P_i) for any mature parr to win against any immature parr and vice versa. The plot shows the median, the upper and lower quartiles and the extremes for the mature and the immature parr, all 12 trials taken together.

$$r_A = \sum_{i=1}^{k} a_i \ast c_i \qquad (1)$$

where r_A is the relative resource value in the good patch, say A, *i* is an ability class among *k* ability classes, a_i is the number of individuals of class *i* going to patch A and c_i is the competitive ability of class *i*. The derivation of eq. (1) is formally given by Houston and McNamara (1988). Several solutions of eq. (1) exists. Let $F(a_p,a_n)$ be the number of ways in which a_p mature parr and a_n immature parr can be assigned to patch A and b_p mature and b_n immature parr can be assigned to patch B. Houston and McNamara (1988) suggested that the different solutions of eq. (1) could be calculated using basic permutation formulae, so that

Table 3. The four possible solutions of eq. (1) when $N_p=9$, $N_n=18$, $r_A=0.8$ and $c_p=0.6$ and $c_n=0.4$. P_A is the proportion of all animals in location A, i.e. the good patch.

Solution	a_p	a_n	$F(a_p,a_n)$	$P(a_p,a_n)$	P_A
1	6	18	84	0.000	0.899
2	7	15	29,376	0.120	0.815
3	8	12	167,076	0.682	0.714
4	9	9	48,620	0.198	0.667

$$F(a_p,a_n)=\frac{N_p!}{a_p! \ast b_p!} \ast \frac{N_n!}{a_n! \ast b_n!} \qquad (2)$$

in which N_p and N_n are the total number of mature and immature parr, respectively. Table 3 shows the results obtained from a simulation of eq. (2). The number of ways in which a_p mature parr and a_n immature parr can be assigned to the good patch is given by $F(a_p,a_n)$. Since every combination of a_p and a_n, given in Table 3, is equally probable to occur, then $F(a_p,a_n)$ divided by the total number of ways gives the probability $P(a_p,a_n)$ of the distribution of a_p and a_n. In the present experimental set up, the resource value (r_A) of the good patch equals 0.8 and, hence, the resource value of the poor patch equals 0.2. The cardinal rank calculation revealed that the competitive ability of the mature parr is about $c_p=0.6$ and about $c_n=0.4$ for the immature parr. Only some combinations of the number of mature and the number of immature parr satisfy eq. (1). One such a combination is 9 mature and 18 immature parr used in this experiment.

Predictions

The distribution derived from H_o suggests that the 9 mature and 18 immature parr should distribute themselves at random, i.e. 4.5 mature parr and 9 immature parr should be found in the good patch. Because the resource value of the good patch is 0.8, the prediction given by H_1 is that 7.2 mature parr and 14.4 immature parr should be found in the good patch. By simulating the model proposed by Houston and McNamara (1988), the predictions derived from H_2 could be calculated. From the results shown in Table 3, the most probable combination of mature and immature parr, satisfying the eq. (1), is 8 mature and 12 immature parr in the good patch, i.e. $P(a_p,a_n)=0.68$.

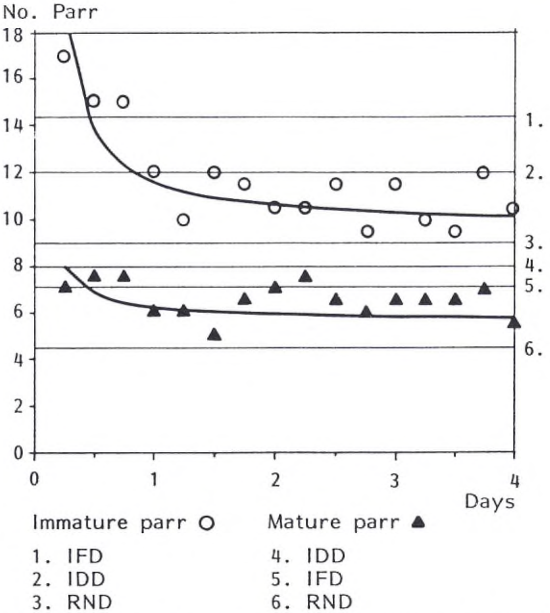

Fig. 4. A S-curve trend analysis of the average number of mature (M) and immature parr (IM) in the good patch, in relation to time. The predicted distributions were randomly (RND), ideal free (IFD) and ideal despotic (IDD).

Results

Based on the average number of parr presented in the good patch, on each inspection and for all trials together, a S-curve trend analysis was constructed

$$S=\exp(a+b/t)$$

in which *a* and *b* is coefficients and *t* is time (Statgraphics v. 3.0, STSC Inc). For mature parr *a* is 1.74 and *b* is 0.43 and for immature parr *a* is 2.27 and *b* is 0.79. A forecast procedure based on the S-shaped growth curve showed that 6.0 (S.E. +/–0.1) mature parr and 10.4 (S.E. +/–0.2) immature parr were occupying the good patch (Fig. 4). Interestingly enough, there was a gradual decline of the numbers of both the mature and the immature parr present in the good patch, although the situation became stabilized during the final two days of each experimental period.

Because the number of both mature (mean=5.8, SD=1.4) and immature (mean=9.8, SD=2.5) flatted out during the two last days, a second way of testing the hypotheses, statistically, was constructed. We found a significantly higher number of parr in the good patch than predicted from the H_0 hypothesis (One sample t-test; Mature parr: $t=7.7$, $df=63$, $P<0.0001$; Immature parr: $t=2.6$, $df=63$, $P<0.05$). There was, however, a significantly lower number of both categories of parr in the good patch than predicted from the H_1 hypothesis (One sample t-test; Mature parr: $t=8.1$, $df=63$, $P<0.0001$; Immature parr: $t=14.5$, $df=63$, $P<0.0001$). The actual numbers of parr present in the good patch was also significantly lower than those predicted from the H_2 hypothesis (One sample t-test; Mature parr: $t=12.8$, $df=63$, $P<0.0001$; Immature parr: $t=6.9$, $df=63$, $P<0.0001$).

Discussion

Maturation and competitive ability

Although there is a strong selection pressure to become a large-sized as a smolt (Lundqvist et al. 1988), many juvenile male parr allocate energy resources into gonad formation during the summer and autumn prior to smoltification, and become sexually mature (Evropeytseva 1960, Österdal 1969, Eriksson et al. 1979). Such an allocation of the available resources in fact entails a reduction in somatic growth and thus probably confers on the parr a reduced Darwinian fitness (e.g. Thorpe and Morgan 1980). However, such a cost, in evolutionary terms, is probably counterbalanced by an increase in reproductive success (Myers 1984, Myers et al. 1986). Not all the males in a cohort of parr become sexually mature, but usually those individuals which are the fastest growers (Alm 1959, Thorpe et al. 1983). They will eventually catch up in body size with the immature parr during smoltification, or just after (Thorpe and Morgan 1980, Skilbrei 1990, Järvi et al. 1991).

Numbers of factors have been assumed to regulate the growth of parr and smolt. Under natural conditions, one may reasonably assume that it is the outcome of the competition for optimal food stations in the rivers which produce the individual variation in growth rate. The results of several experimental studies on salmonids have in fact demonstrated an association between growth and rank dominance (e.g. Symons 1971, Fernö and Holm 1986, Holm and Fernö 1986, Metcalfe 1986, Davis and Olla 1987). Although the mature parr used in our experiments were significantly smaller than the immature ones, they possessed the better competitive ability. Thus, competitive ability does not seem to be primarily associated with size per se, but rather with a phenotypical viability factor. Such a factor affects fighting ability so that the mature parr can secure a greater proportion of the available resources in any food patch, which thus has a secondarily effect on their growth.

Resource sharing between mature and immature parr

The experimental difference in the resource value of the available patches affected the distribution of the parr in the patches as shown by the significantly greater number of both mature and immature parr present in the good patch. Thus, the H_0 hypothesis can be rejected.

Due to differences in competitive ability the premises for the IFD theory were violated in this experiment. However, the parr would have been distributed according to a true IFD had the relative pay-off-sum learning rule been adopted (Regelmann 1984). Regelman's rule has been applied to some experimental results. Regelman (1984) suggested that the results obtained from Harper's (1982) ideal free duck experiment could be due to such a learning rule. The mallards, *Anas platyrhynchos*, quickly distribute themselves between the two food patches in a good approximation with the patch profitability. The premise for a true IFD was violated, however, since competitive abilities of the mallards differed (Harper 1982). In a food patch choice experiment, Milinski (1984) showed that subordinate three-spined stickleback, *Gasterosteus aculeatus*, did not settle until the dominant conspecifics had made their choice.

Despite that, the final distribution did not differ from IFD and thus Regelman's learning rule could be operative in certain cases. In our study, the frequency of parr in the good patch was quite high during the initial first day of each experiment, and in fact did not differ from IFD. However, after the fish had settled, the proportions of both mature and immature declined significantly in the good patch. Hence, the ultimate numbers of parr present in the good patch were significantly lower than those predicted from the IFD theory. Thus, the H_1 hypothesis can be rejected.

The results of the resource sharing experiments showed that only 61 % of the fish were present in the good patch, instead of the 74 % predicted from the IDD model. The simulation also showed that there should have been an over representation of both mature and immature parr in the good patch. On average, only 6 of the predicted 8 mature parr were observed in the good patch, while only 10 out of predicted 12 immature parr were observed. Thus, the H_2 hypothesis can be rejected.

A number of factors could explain this underusage of the good patch:

1) It is obvious that if c_i does not equals P_i, the simulation is not sound. However, since mature parr both grow faster and are dominant over immature parr, it is reasonable to assume that P_i is a good assessment of c_i. In fact, in an artificial stream experiment Symons (1971) showed that the average growth-rate of the subordinates was about two-thirds of that of dominants, i.e. the same difference as found in P_i between mature and immature parr in our experiment. Hence, it seems reasonable to assume that P_i represents a good approximation of c_i for the ability class.

2) During the parr stage, the Atlantic salmon is assumed to be territorial, and the drift of food should have little immediate effect on the abundance of territorial parr (e.g. Kalleberg 1958, Symons 1971, Wankowski and Thorpe 1979). Resource-independent territoriality, of course, would entail an under-exploitation of the good patch. Two different factors have an impact on the tendency for territoriality, viz., the size of the parr and the stream velocity (Kalleberg 1958, Symons 1971, Wankowski and Thorpe 1979). In order to reduce such a tendency we used a rather low stream velocity in the tank and, in addition, the parr were rather large-sized, since they were expected to smoltify during the spring. Thus, it is reasonable to assume that the tendency for territoriality would have been low. However, as the parr were not individually marked, we could not record the actual number of territorial individuals.

3) Abrahams (1986) has shown that perceptual constraints might result in an under-usage of the good patch, even without differences in competitive ability. Houston and McNamara (1988) suggested that the statistical mechanic model should be modified to allow for perceptual error, resulting in a weaker constraint. A combination of the statistical effect and the perceptual limitations would produce a very marked under-usage of the good patch (Houston and McNamara 1988).

4) In our experiment, we divided the parr into two competitive ability classes, viz., mature and immature parr. The results in Fig. 3 show that there is a marked and skewed variation in the competitive ability of the two categories of parr. Such a skewed variation in competitive ability within an ability class implies that the outcome of each pair-wise interaction will not have been equal for the competitors involved (Table 1, Fig. 3). However, how such a skewed distribution of competitive ability, within an ability class, affects the simulation model, is outside the scope of this paper.

Acknowledgments

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Age Determination of Arctic Charr (*Salvelinus alpinus*) from Surface and Cross Section of Otoliths Related to Otolith Growth

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Abstract

Ages, determined from otolith rostrum by lateral view and from cross sections of burned otoliths of two sympatric Arctic charr (*Salvelinus alpinus*) morphs from Bear Island (74°30′N), were compared. The cross section method is recommended for old fish from stunted populations, especially if the otoliths are unclear. In charr older than 10 years from the slow growing morph, otolith sections gave significantly higher ages than the lateral otolith views. However, the underestimations of ages, using lateral views, were small compared to other studies of Arctic freshwater fishes and marine fish species. The correspondence to fish length growth is stronger for otolith rostrum growth than for growth in otolith thickness. Despite this, annual rostrum growth seems to be higher than otolith thickness growth throughout the whole lifespan. Therefore, allometric otolith growth is probably not the reason for higher cross sectional ages. A better uncovering of the innermost zones by the cross section method and the better contrast obtained by this method is assumed to be the explanation. The analysis indicate that age itself, by some endogenous biological rhythm, affects otolith size. A direct linear relationship between otolith thickness and age opens the possibility of age estimation based on otolith measurements.

Introduction

By use of cross sections of otoliths for age determination, as compared to age determined from the otoliths external surface, significantly higher ages for old individuals are obtained for many fish species (Macer 1968, Blacker 1974, Power 1978, Beamish 1979 a, b, Chilton and Beamish 1982, Barber and McFarlane 1987, Beamish and McFarlane 1987, Fujiwara and Hankin 1988). This is explained by allometric otolith growth. In old fish with a stagnant length growth, otolith depositions occurs predominantly on the internal surface (sulcus acusticus side). Therefore lateral views will not reveal all growth zones.

Using otolith cross sections Power (1978) recorded ages close to 60 years in Arctic populations of whitefish (*Coregonus clupeaformis*). Comparing these results with those obtained from lateral otolith views, Power documented underestimations of age of up to 20 years in old fish. He hypothesised that similar aging error might occur in data from other Arctic populations of freshwater fishes, and that this could have significant impact on estimats of growth and mortality.

Arctic charr (*S. alpinus*) is the most abundant species in the European Arctic. Age of Arctic charr is usually determined by lateral views of the otolith. By this method one might expect underestimations of age in Arctic populations of the species, compared to age determined from cross sections of otoliths. The aim of the present study was to test this hypothesis and to examine how otolith growth affects age determination.

Material and methods

In 1978 Arctic charr was captured by gillnets in Lake Ellasjøen at Bear Island (74°30′N) between Spitzbergen and Norway. Ellasjøen is a subpolar, cold monomictic lake (Klemetsen at al. 1985). Arctic charr is the only fish species present. The charr is segregated into two morphs, in the following referred to as lower and upper mode charr. The two morphs differ in growth rate, size and age at maturity, longevity, spawning colouration, morphology, number of gill rakers and pyloric caecum, sex ratios and fecundity, but cannot be seperated by frequencies of Est-2 alleles (Klemetsen et al. 1985). Generally, fork lengths were <20 cm for ripe lower mode charr and >30 cm for ripe upper mode charr.

Age determination

The whole material (n=1,312) was first aged using a lateral view of the otoliths external surface (Figs. 1 and 2). The otoliths were viewed immersed in glycerol, on a black substratum, using a binocuar microscope (magnification 6–50 times) and reflected light. The otoliths were clear, especially in young and upper mode charr, and age was determined without any further preparation.

The number of zones varied along different axes in the surface. Usually, it was easiest to identify the zones along the rostrum (Figs. 1 and 2), and in old fish the rostrum gave the highest age (Kristoffersen 1982). This is in accordance with the results of Nordeng (1961). Consequently, the rostrum was used for age determination from the lateral surface. These ages are later referred to as lateral ages.

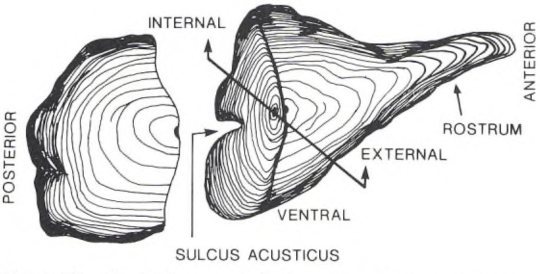

Fig. 1. Sketch of charr otolith showing position of the section and terminology used.

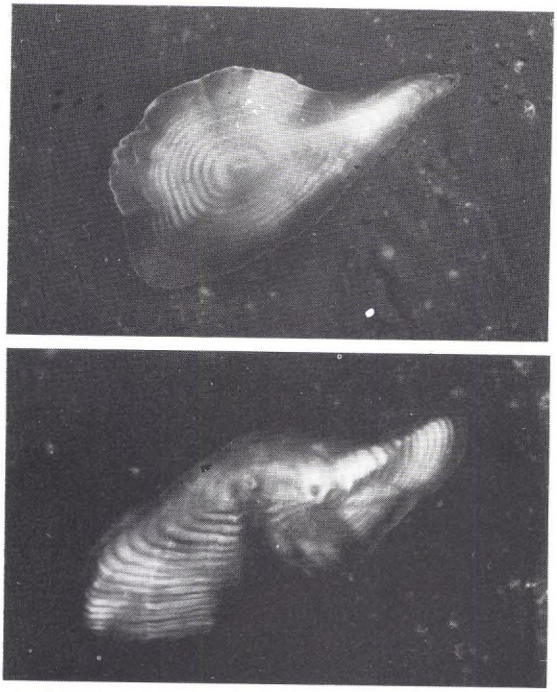

Fig. 2. Otolith of 17 year old upper mode charr. Lateral view of external surface (above) and cross section.

From lateral age-, length- and maturity distributions (Kristoffersen 1982), and the other criteria which differ between the two morhps (c.f. above), samples of lower mode charr and upper mode charr were selected for more detailed analysis of age and otolith growth. Separating the two morphs was possible, however, only above a minimum age (Kristoffersen 1982). For both morphs, 10 fishes from each year class were selected at random. If a year class contained less than 10 fishes, all fishes were included in the sample.

Totals of 102 lower mode charrs older than 5 years (lateral age) and 116 upper mode charrs older than 9 years (lateral age) were aged from otolith cross sections. Otolith rostrum length and otolith thickness were measured in 84 lower mode charrs and 130 upper mode charrs. The discrepancy between numbers aged and numbers measured in lower mode charr is due to damage of some otoliths and in some cases to problems connected with exact identificaton of the centre and rostrum peak on the photographs (c.f. Measurements). In upper mode charr these problems were less, and there was usually sufficient material to supplement the sample if necessary. In order to obtain as good data as possible for the regression analysis, the upper mode charr sample was extended with two more year classes (8 and 9) when doing the measurements.

Slightly modified, the technique of Power (1978) and Christensen (1964) was used for age determination from otolith cross section. The otoliths were placed on a hot plate and burned brown in 20–40 seconds. They were then dropped into 96 % ethanol for about two minutes and broken through the nucleus, along the dorsoventral axis (Figs. 1 and 2). The halves were supported in dark plasticine and studied as described for whole otoliths.

The zones were easiest to identify in the internal ventral part of the section (Figs. 1 and 2), and in old fish this part showed the highest age. This is in accordance with the results of Beamish (1979a) for Pacific hake (*Merluccius productus*). Consequently cross sectional ages were determined from the internal ventral part.

Only distinct hyalin zones were interpreted as annuli. Sometimes both lateral surface and cross section showed some very narrow and less continuous hyalin bands. These were interpreted as checks (not true annuli). Such interpretation of zones by reference to certain master images is an important part of age determination (Sych 1971, 1974). This gave a varying degree of uncertainty in the age determinations (Kristoffersen 1982), and also an amplitude of deviation in repeated agings by the same method. Only when cross sectional ages were significantly higher than lateral ages, were the cross sectional ages preferred in further analysis. The Wilcoxon signed-rank test with correction for ties (Lehmann 1975) was used to test for differences between the two aging methods.

Precision in the age determinations was tested by repeated aging by the same method. The within-method agreement was reasonably good (Kristoffersen 1982). Even for the cross section method, where the precision was lowest, agreement was within +/–1 year for 84.1 % of the otoliths, and there was no statistically significant difference between repeated agings.

Measurements

The lateral surfaces of the otoliths were photographed through a binocular microscope by a Wild MPS 20 Semiphotomat camera and polaroid 3,000 ASA black/white positive film. Magnification was 23.2 times for lower mode charr otoliths and 15.8 times for upper mode charr otoliths. Otolith rostrum length (distance between centre and rostrum peak) was measured on the pictures to the nearest 0.1 mm. Thickness (maximum external-internal distance) was measured to the nearest 0.01 mm directly on the otolith using a micrometer (Fig. 1).

Measurement error was studied by making 10 independent measurements of otoliths of different size. Relative error was of the same magnitude for rostrum length and thickness, within the range of 0.76–0.85 % (Kristoffersen 1982). The measurements were, therefore, considered a reasonably good expression of biological variation. Correlation and regression analysis follows the methods of Sokal and Rohlf (1969).

Results

Age determination

Lower mode charr

In the sample of lower mode charr, ages varied between 6 and 18 years according to the lateral aging method, and between 5 and 24 years according to the cross section aging method (Fig. 3). The two methods gave the same results in 53.9 % of the sample. The cross section method gave a higher age for 37.3 % and a lower age for 8.8 % of the fish. The cross sectional ages were significantly higher than the lateral ages when the whole group was tested ($Vs=4.48$, $p<<0.001$). Accepting cross sectional ages as true ages for lower mode charr (c.f. Material and methods, and Discussion), the frequency and size of deviations increased with increasing age (Fig. 4). Charr younger than 10 years did not show significantly higher cross sectional ages ($Vs=-0.38$, $p=0.648$). In the age group 10–13 years, and for charr older than 13 years the cross section method gave significantly higher age than the lateral method ($Vs=2.57$, $p=0.005$ and $Vs=4.28$, $p<<0.001$).

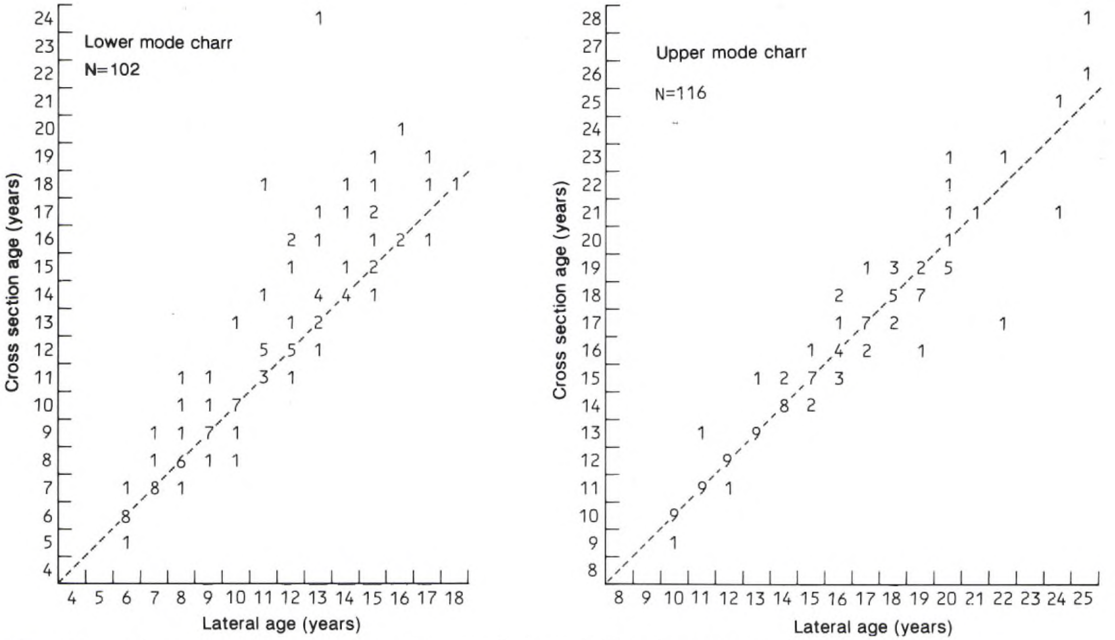

Fig. 3. Comparison of lateral age and cross section age for lower (left) and upper mode charr.

Upper mode charr

In the sample of upper mode charr, ages varied between 10 and 25 years according to the lateral method, and between 9 and 28 years according to the cross section method (Fig. 3). The two methods gave identical results in 61.2 % of the sample. The cross section method gave a higher age for 16.4 % and a lower age for 22.4 % of the fish. The cross sectional ages were not significantly higher than the lateral ages when the whole group was tested (Vs=–0.83, p=0.797). The deviations increased with increasing age (Figs. 3 and 4), but even for old upper mode charr (age groups 14–17 years and >17 years) the age differences were not significant (Vs=0.17, p=0.433 and Vs=–1.18, p=0.881). Neither did mature fish (n=36) have significantly higher cross sectional ages (Vs=0.00, p=0.500).

Otolith growth

The relationship of fish length to age was curvilinear for both lower and upper mode charr. However, ln-transformation gave a linear relationship for both morphs (Fig. 5). The two variables were significantly correlated, and linear regression analysis (Table 1) and comparation of regression coefficients was possible. The coefficient of regression was significantly higher for upper mode charr than for lower mode charr (t=12.34, p<<0.005).

The relationship of otolith rostrum length to age was also curvilinear in both morphs, as was fish length to age, and ln-transformation gave a linear relationship (Fig. 5, Table 1).The coefficient of regression was significantly higher for upper mode charr than for lower mode charr (t=8.11, p<<0.005).

The relationship of otolith thickness to age showed direct linearity for both morphs (Fig. 5, Table 1). The coefficient of regression was significantly higher for upper mode charr than for lower mode charr (t=4.47, p<0.005).

Unlike otolith thickness, annual growth of otolith rostrum obviously decreased in old charr, as did annual fish length growth. Annual rostrum growth was, nevertheless, higher than annual

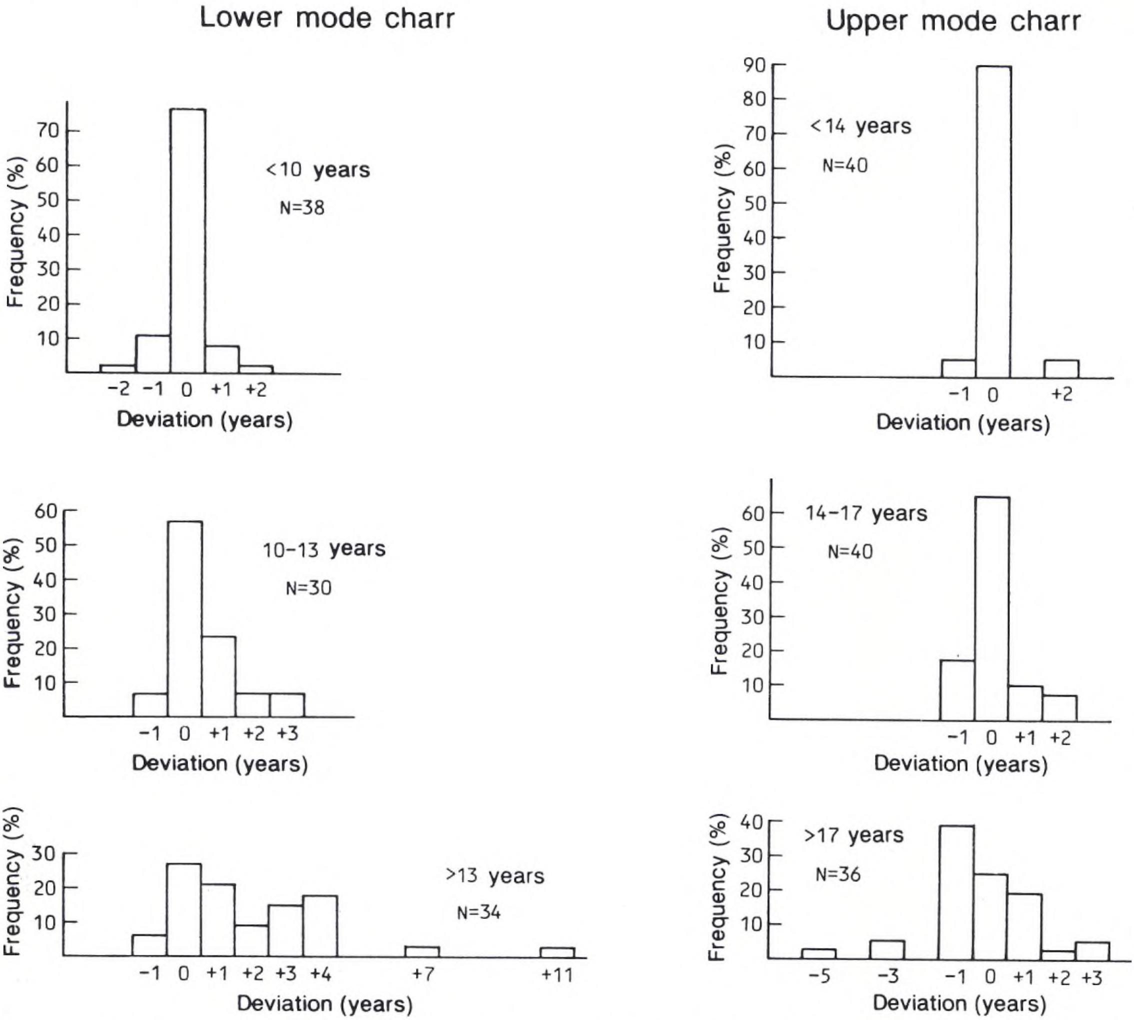

Fig. 4. Deviation in age determination from the lateral to the cross section method in different age groups of lower (left) and upper mode charr.

growth in thickness throughout the whole lifespan. Estimation according to the equations of regression (Table 1) gave similar annual growth in thickness and rostrum at age 23.3 years for lower mode charr and at a theoretical age of 42.9 years for upper mode charr.

There was a linear relationship between otolith rostrum length and fish length, and between otolith thickness and fish length (Fig. 6, Table 1). Although rostrum length followed the fish length growth pattern, the coefficient of regression for the relationship between rostrum length and fish length was significantly higher for lower mode charr than for upper mode charr ($t=2.79$, $p<0.05$). The relationship, otolith thickness/fish length, showed even more distinct differences between the two morphs. Corresponding test of size of regression coefficients gave $t=3.17$ and $p<0.005$.

Discussion

For upper mode charr there were no significant differences between ages determined from cross

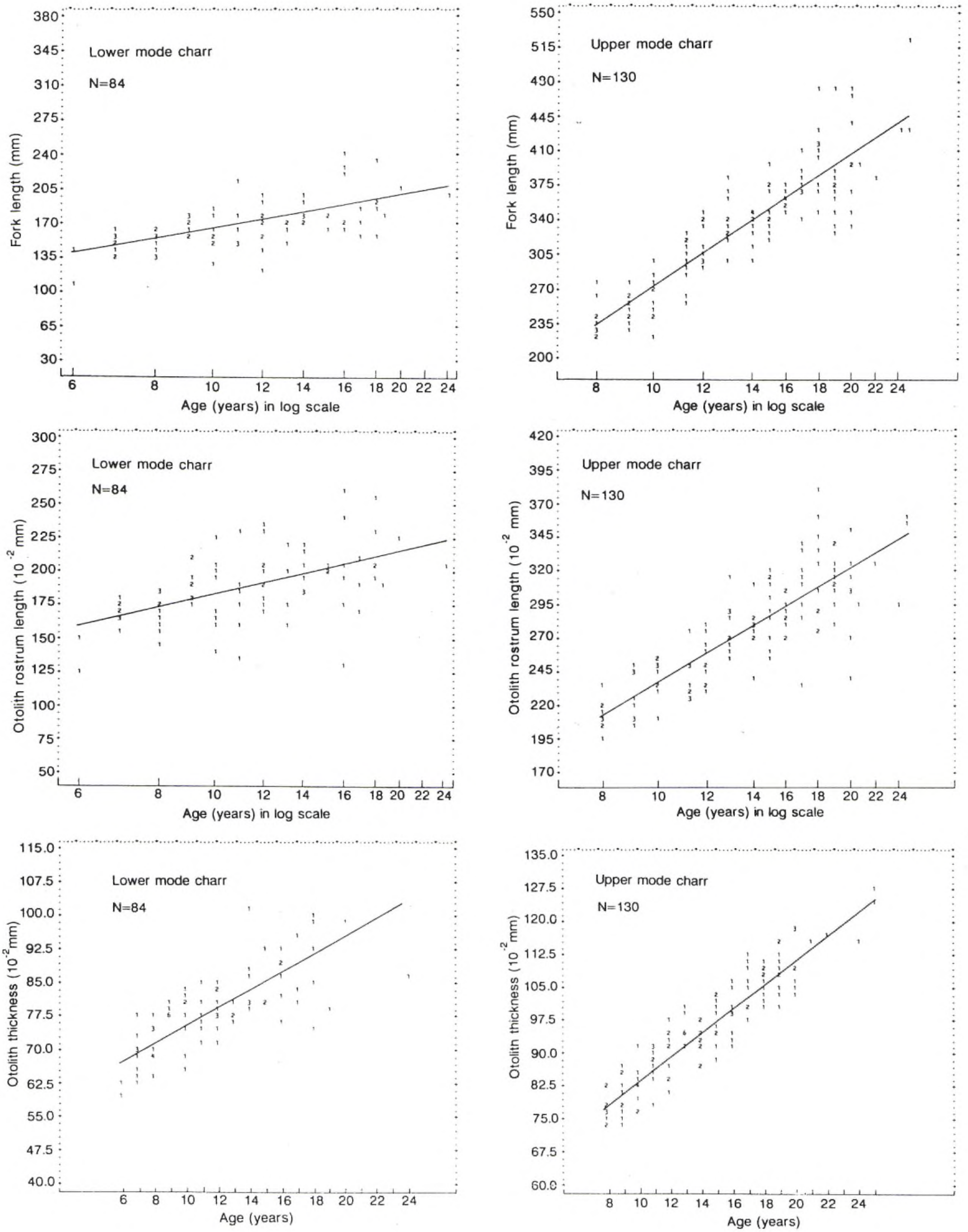

Fig. 5. Relationship of fish length (fork length), otolith rostrum length and otolith thickness to age for lower (left) and upper mode charr. ——— = regression line (c.f. Table 1).

Table 1. Correlation and regression analysis of different relationships for lower mode charr (LMC) and upper mode charr (UMC). Fl = fork length (cm, mm where *), Rl = otolith rostrum length (mm), Th = otolith thickness (mm), ln = natural logarithm, A = age (years), r = coefficient of correlation, t = test size and p = propability of significance.

Relationship	Charr morph	Correlation			Regression line
		r	t	p	
Fork length/age	LMC	0.63	9.25	<<0.001	Fl = 5.46 + 4.67 lnA
	UMC	0.89	30.47	<<0.001	Fl = –15.30 + 18.62 lnA
Rostrum length/age	LMC	0.58	8.14	<<0.001	Rl = 0.757 + 0.468 lnA
	UMC	0.88	28.61	<<0.001	Rl = –0.393 + 1.205 lnA
Otolith thickness/age	LMC	0.83	17.81	<<0.001	Th = 0.554 + 0.020 A
	UMC	0.93	40.18	<<0.001	Th = 0.554 + 0.028 A
Rostrum length/ fork length	LMC	0.75	13.63	<<0.001	Rl = 0.498 + 0.0082 Fl*
	UMC	0.86	25.85	<<0.001	Rl = 0.873 + 0.0056 Fl*
Otolith thickness/ fork length	LMC	0.74	13.01	<<0.001	Th = 0.347 + 0.0026 Fl*
	UMC	0.88	28.74	<<0.001	Th = 0.367 + 0.0018 Fl*

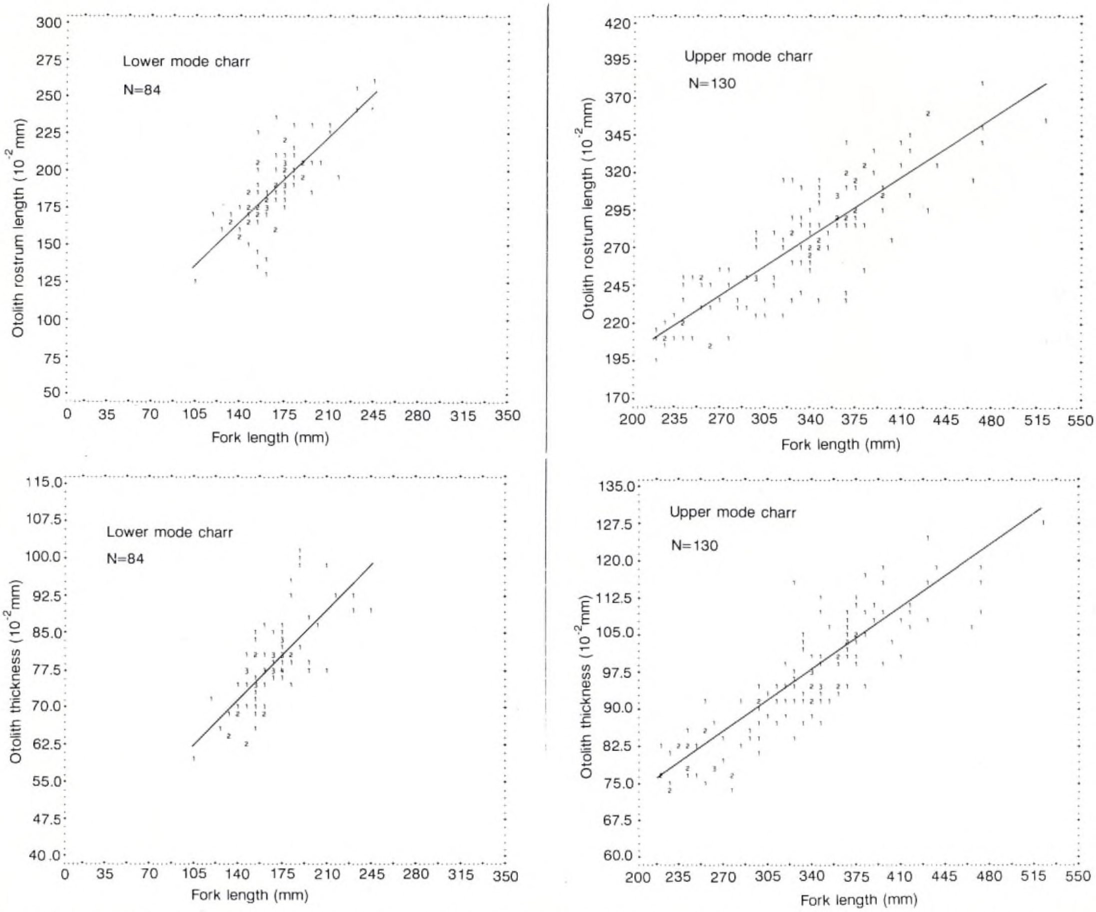

Fig. 6. Relationship of otolith rostrum length and otolith thickness to fish length (fork length) in lower (left) and upper mode charr. ——— = regression line (c.f. Table 1).

sections of otoliths and ages determined by lateral otolith views. In contrast, the cross section method gave significantly higher ages than the lateral method for old lower mode charr. However, the underestimation of lateral age was small compared to the aging error reported for Arctic charr from Alaskan and Canadian waters (Barber and McFarlane 1987), Arctic populations of whitefish (*C. clupeaformis*) (Power 1978) and for some marine species (Beamish 1979a, b, Chilton and Beamish 1982, Beamish and McFarlane 1987, Fujiwara and Hankin 1988). The cross section method should, nevertheless, be used for old fish in stunted populations of Arctic charr, especially if the otoliths are unclear.

Power (1978) gives no information about which part of the otolith he used for lateral age determination. Barber and McFarlane (1987) determined lateral otolith age of old Arctic charr from what they misleadingly call "the otolith's dorsal surface". Based on their figures, this corresponds to the posterior otolith half (Fig. 1).

In our study, otolith rostrum was used for lateral age determination. This is probably the reason for the small discrepancy between lateral and cross sectional age. Lateral aging from rostrum also minimizes the error in growth and mortality rates, suggested by Power (1978) and supported by Barber and McFarlane (1987).

A limited validation of the age determinations was made possible due to a biological tag. In lateral view of otoliths of growing fish of intermediate age, an unusual narrow opaque zone appeared with three hyalin zones, two "normal" opaque zones and one not yet complete opaque zone outside. This unusual narrow opaque zone was probably deposited the summer 1975, when the air temperatures at Bear Island were extremly low (Kristoffersen 1982). Based on this assumption, it was confirmed for most intermediate old fish, that the outermost zones, interpreted as annuli by the lateral method, were true annuli. Corresponding validation of lateral age of old fish was not possible. Nor was it possible to identify the special features of the 1975 summer zone in the otolith cross section.

In a lateral view of clear otoliths at least the first 5–6 annuli could be identified along the dorso-ventral axis, where the otoliths grow very slowly. By gradually tilting broken otoliths, to obtain latero-transverse views, it could be confirmed that the inner zones corresponded in lateral surface and section. This correspondence was seen both in burned and unburned otoliths, confirming that also the section shows an annual formation of zones. The cross sectional ages can, therefore, be accepted as true ages. For some marine species the validity of cross sectional age has also been proven by mark-recapture studies (Beamish and Chilton 1982, Beamish et al. 1983, Beamish and McFarlane 1987).

Cessation of otolith growth in length and height (posterior – anterior and dorso – ventral axes in Fig. 1) for old fish while the otolith continues to grow in thickness, is the usual explanation for higher age estimations from otolith cross sections as compared to lateral surface of otoliths (Macer 1968, Blacker 1974, Power 1978, Beamish 1979a, Chilton and Beamish 1982, Barber and McFarlane 1987, Beamish and McFarlane 1987, Fujiwara and Hankin 1988). In spite of this, it does not appear to have been demonstrated that annual otolith growth in old fish is greater in the cross section than in the lateral dimension used for age determination.

With a few exceptions, (Beamish 1979a, Boehlert 1985, Fujiwara and Hankin 1988), age determinations have not been accompanied by otolith measurements. Often, the conclusion that lateral otolith age is underestimated in old fish because of the above mentioned allometric otolith growth, is based merely on appearence of zones in photographs of the otolith sections (Macer 1968, Blacker 1974, Power 1978, Beamish and McFarlane 1987, Barber and McFarlane 1987). This is valid only if lateral ages are determined along the dorso-ventral dimension (Fig. 1), represented in the cross section photographs. However, in a lateral view, the zones are easiest to identify along an otolith axis having rapid growth. In most species, and obviously in salmonids, this is not the dorso-ventral dimension.

Our study demonstrates that annual rostrum growth was higher than annual growth in otolith thickness throughout the whole lifespan for upper mode charr. Annual growth in otolith thickness could approach annual rostrum growth only in the oldest lower mode charr. However, the measurements of otolith thickness include growth in two directions from the nucleus, and only deposition on the internal surface (sulcus acusticus side) affects cross sectional age. Although external depositions are small (Fig. 2), the measurements indicate that annual deposition on the internal surface is less than annual rostrum deposition also for old lower mode charr. Allometric otolith growth does probably not, therefore, explain the higher cross sectional ages.

Clearness of the otoliths and uncertainty of the age determinations was studied by Kristoffersen (1982). It was the unclear otoliths, often with a high degree of uncertainty when using the lateral method, that had the highest discrepancy between lateral and cross sectional ages. A better uncovering of the innermost zones in unclear otoliths when using the cross section method, and a better contrast by this method, is probably the reason for the higher cross sectional ages in lower mode charr. The better contrast was especially useful in the outer part of the otoliths of old mature lower mode charr. In the lateral view a hyalin tinge of this part of the otoliths made it difficult to identify the zones. In upper mode charr, however, the otoliths were so clear that all zones were identified also by the lateral method.

Uncoupling of somatic and otolith growth rate occurs in fishes under certain circumstances (Marshall and Parker 1982, Mosegaard 1986, Mosegaard et al. 1988, Secor and Dean 1989, Wright et al. 1990). Nevertheless, it is generally accepted that fish length growth, or at least some factor correlated to this, affects otolith growth. The present study supports this, and also that the strength of the correspondence to fish length growth differs in different parts of the otolith.

The correspondence is stronger between otolith rostrum growth and fish length growth than between otolith thickness growth and fish length growth. However, even the rostrum lenght/fish length relationship differs between two charr morphs having different length growth. This may reflect that the otolith size/fish size relationship depend on fish growth rate and metabolic modifiers (Mosegaard 1986, Mosegaard et al. 1988, Secor and Dean 1989, Wright et al. 1990). But it may also indicate that age itself, by some endogenous biological rhythm, affects otolith size, as is earlier suggested based on studies of daily growth zones in otoliths (Mugiya et al. 1981, Radtke and Dean 1982, Campana and Nielson 1985, Secor and Dean 1989). Attention is, therefore, nessessary in back calculating fish length from otolith dimensions.

The age effect on otolith size seems strongest for otolith thickness. The direct linear relationship between otolith thickness and age is in accordence with the results of Fujiwara and Hankin (1988) for sablefish (*Anopolopoma fimbria*). The especially good fit of this relationship for upper mode charr (Fig. 5, Table 1) also demonstrates the posibility of age estimation based on otolith measurements. Further work on aging, based on measurements of otoliths and other hard structures, such as that of Boehlert (1985) using multiple regression models, may replace subjective aging criteria (Sych 1971, 1974) by objective ones.

Acknowledgments

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Effects of Temperature, Season and Feeding Conditions on the Rheotactic Behaviour of two Stocks of Landlocked Arctic Char

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Abstract

The rheotactic behaviour of two-year-old Arctic char from Lakes Visjön and Hornavan was studied during the period February–June in circular stream tanks with infrared photocells. During the first four months of the experiment, upstream movements accounted for 50 % or less of the swimming activity of Lake Visjön char, i.e. most of the swimming activity was directed downstream. In June, however, upstream movements became dominant. The Hornavan char on the other hand, oriented their swimming downstream during most of the experiment but particularly in June. A gradual increase in water temperature played an important role in stimulating these rheotactic responses. Season had an effect on rheotactic behaviour, i.e. the fish response to a rise in temperature increased between February and May. The results also indicated a stronger rheotactic response to increasing temperature in fish fed reduced rations than in fish fed surplus rations. The upstream movements in Lake Visjön char recorded in this laboratory study agree with field observations indicating that this population undertakes upstream exploratory migrations during periods of increasing water temperature in spring.

Introduction

The existence of distinct migration periods in salmonids is well documented. Juveniles of anadromous populations are known to undertake seaward migrations during spring and early summer (reviews in Northcote 1978, Randall et al. 1987). Also freshwater dwelling salmonids leave rearing areas for feeding in another habitat. Grayling (*Thymallus thymallus*), brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), cutthroat trout (*Oncorhynchus clarki*), Arctic char (*Salvelinus alpinus*) and brook char (*Salvelinus fontinalis*), are known to shift between rearing areas in streams and feeding habitats in lakes (Gustafson 1949, Stuart 1957, Northcote 1962, Raleigh and Chapman 1971, Johnson 1980, Power 1980).

As in anadromous salmonids, the migratory pattern of freshwater salmonids may vary between populations of the same species, even within the same geographic area. For example, intraspecific differences in migratory behaviour have been documented between inlet and outlet spawning populations of several salmonid species, with fry/juveniles in the outlet stream inclined to swim upstream and vice versa for those in the inlet (Raleigh 1967, Raleigh and Chapman 1971, Brannon 1972, Kelso and Northcote 1981, Kaya 1989). Thus, the migratory behaviour of such populations appears to reflect genetically and environmentally influenced responses to water current (Arnold 1974, Kelso et al. 1981, Kaya 1989).

Previous field studies have documented extensive upstream migrations in the landlocked Arctic char population of Lake Visjön, an oligotrophic lake in northwest Sweden (Näslund 1990, 1991). The period of migration was restricted to about two weeks in May–June in connection with spring floods. Creeks with higher water temperature were preferred over colder creeks. First time migrants were two- or three-year-old juveniles with lower condition factor than lake resident char of the same age. Upstream migrations in juvenile Arctic char during spring have been documented previously (Craig and Poulin 1975, Johnson 1980), in sharp contrast to the downstream migrations normally observed in anadromous stocks during this time of the year (cf. Johnson 1980).

The research reported here was designed to determine whether the migratory behaviour of Lake Visjön char is also expressed under experimental conditions in circular stream channel tanks, in which case it could be considered genetically influenced. Effects of season, water temperature and food supply on the species' migratory behaviour were also tested. Furthermore, Lake Visjön char were compared with a behaviourally contrasting char population, the Hornavan char. It is a landlocked stock that is known to behave like anadromous char, i.e. change over to a negative rheotaxis during spring (Schmitz 1991).

Material and methods

Lake Visjön is a small (2 km^2), shallow (max depth 3 m) lake situated in a subarctic area in the northwest part of Sweden (see Näslund 1990 for description). Visjön char are insectivorous and spawn in the lake during early September. Arctic char eggs from 25 females were fertilized with sperm from 8 males from Lake Visjön on 10 September 1985 and transported immediately to the Fisheries Research Station at Kälarne (63°00'N, 16°05'E) in central Sweden.

Lake Hornavan is a large (about 500 km^2), deep (max depth 122 m) lake in north Sweden. Hornavan char are fast growing and become piscivorous. Spawning takes place in the lake in September–October. Fertilized eggs from the Hornavan stock were collected from a brood stock available at the Department of Aquaculture, Swedish University of Agricultural Sciences. These eggs represented second generation hatchery stock.

After hatching in April 1986, the juveniles were raised in ordinary rearing tanks (1 × 1 m) under ambient (Lake Ansjön, Kälarne) temperature conditions. The fish were fed conventional dry pellet food (EWOS) in surplus until December 1987. At the start of the experiment, in January 1988, two groups of each stock, each consisting of 70 individuals, were formed and placed in individual tanks. The initial mean sizes of the Visjön char (205 g and 25.8 cm) and the Hornavan char (237 g and 24.9 cm) were about the same. One group of each stock was fed surplus rations of dry food in accordance with the manufacturers' (EWOS) recommendation, while the other was fed reduced rations of dry food, representing about 50 % of the recommended ration.

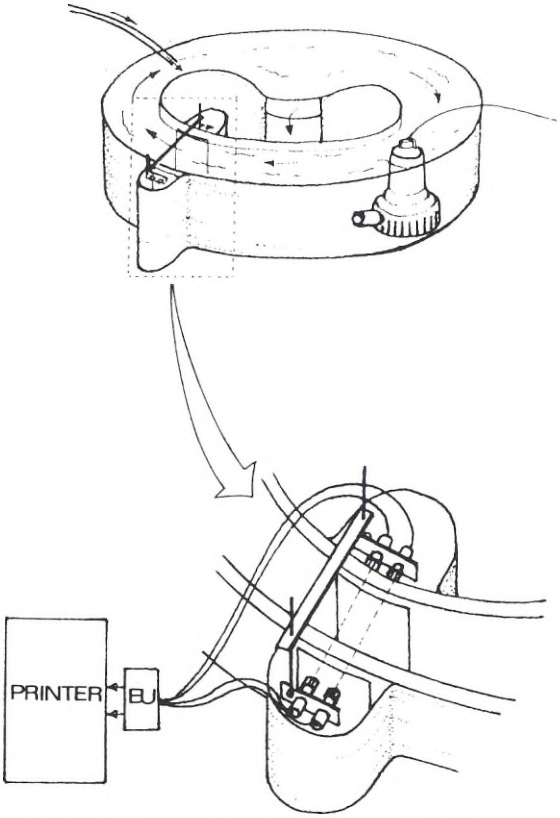

Figure 1. Circular stream tank with infrared photocells.

Swimming direction was measured in circular (1 m diameter) stream tanks (Fig. 1). The tanks received a continuous flow of natural water (3 l min^{-1}). E-heim pumps created a current of 0.5 m s^{-1} near the bottom in the narrow part of each tank (Fig. 1). Fish passages were recorded by a double set up of infrared photocells (Visolux). Upstream and downstream movements were registered on separate channels on a time printer (Elmeg), recording the numbers of passages per hour (see Eriksson and Lundqvist 1982).

The experiment was run with representatives of the four groups of fish (Visjön and Hornavan fed surplus and reduced rations) from 1 February to 30 June 1988 under natural light conditions. Each month was divided into two experimental

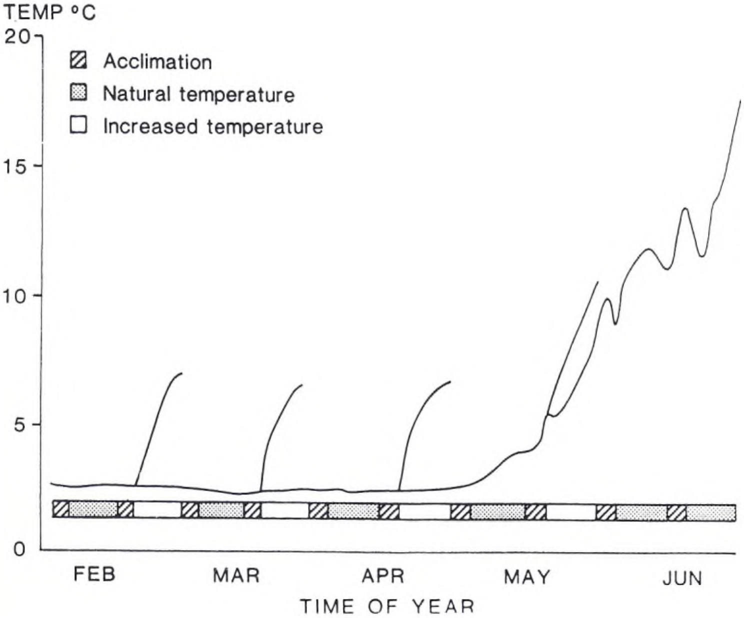

Figure 2. Temperature conditions in the circular stream tanks. Temperature was increased during days 20–30 each month, except in June.

periods, consisting of 5 days of acclimation and 10 days of recording. Six fish were used in each of four stream tanks (one tank for each group). The fish were replaced at the start of each 15 day period. During the first period (days 1–15) each month, the experiment was run under natural temperature conditions (Fig. 2). During the second period (days 16–30 of each month) the temperature was gradually increased, a total of 4–5°C after the 5 day acclimation period (Fig. 2). Due to high natural temperatures, no artificial increase in temperature could be arranged during the second period in June. In addition, because of a photocell failure, observations during 16–30 June on Hornavan char fed reduced rations could not be completed.

Results

For Visjön char fed surplus rations and kept under natural temperature conditions, a shift over to predominantly upstream movements was recorded in the first part of June (Fig. 3a). The proportion of upstream movements during this period was significantly higher than for the preceding months ($p < 0.05$, Analysis of variance). For fish kept under increasing temperature, a similar shift was observed in May, again with significantly more upstream movements than for previous months ($p < 0.05$, Analysis of variance). For Hornavan char fed surplus rations the direction of the swimming activity under natural temperature conditions was mainly oriented downstream, although it varied considerably (Fig. 3b). The proportion of downstream movements was significantly higher in the increased temperature group than in the natural temperature group during all months except February ($p < 0.05$, Analysis of variance).

Visjön char fed reduced rations mainly swam downstream during the period February–May under natural temperature conditions (Fig. 3c). By contrast, in both experimental periods in June, upstream movements were predominant and differed significantly from the preceding four months ($p < 0.05$, Analysis of variance). In low ration Visjön char an artificial rise in temperature tended to induce a shift towards upstream movements as early as April.

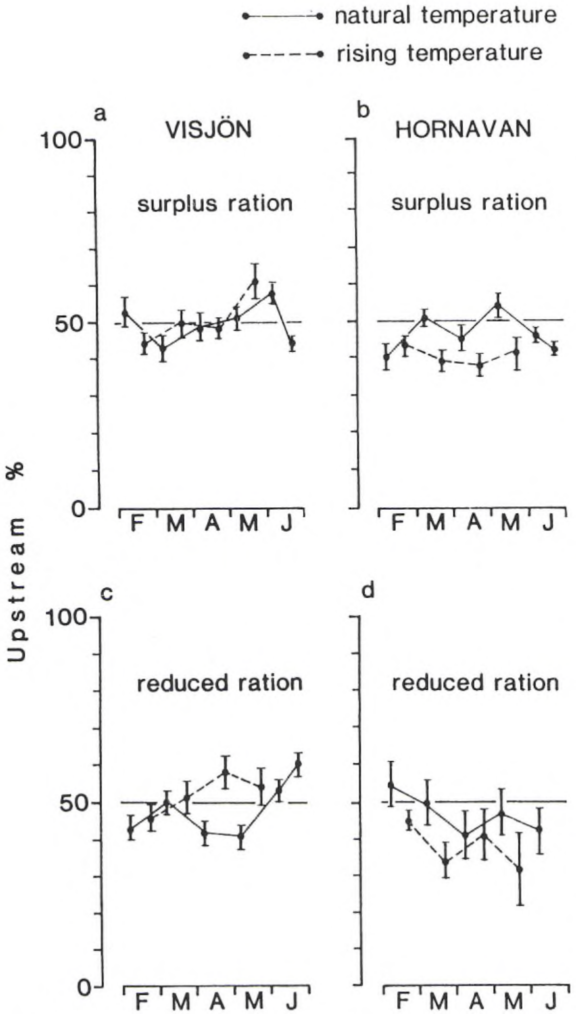

Figure 3. Swimming direction in Arctic char, February–June 1987, given as relative proportion of upstream passages (mean ± 2 S.E. for 10 day periods). a – Visjön char, surplus ration, b – Hornavan char, surplus ration, c – Visjön char, reduced ration, d – Hornavan char, reduced ration.

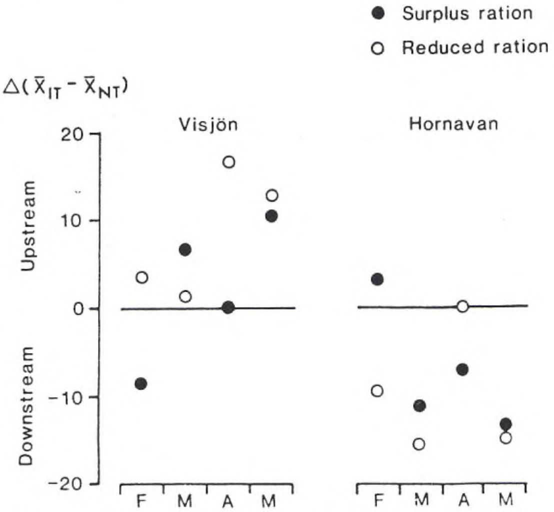

Figure 4. Effects of temperature on swimming direction in Visjön and Hornavan char, February–May 1987. Percentage of passages directed upstream (mean for 10 days) during a period of increasing temperature minus the corresponding percentage (mean for 10 days) under natural temperature conditions within the same month.

In Hornavan char fed reduced rations, upstream movements accounted for 40–55 % of all passages during the experiment (Fig. 3d). In contrast to Lake Visjön char, low ration Hornavan char tended to increase their proportion of downstream movements if kept under increasing temperature (Fig. 3d). The difference between the increased temperature and natural temperature groups was significant during February, March and May ($p < 0.05$, Analysis of variance).

To illustrate the effects of a temperature increase, the differences in swimming response between fish subjected to an artificial increase in temperature and fish kept under a natural temperture regime during the same month was calculated (Fig. 4). Visjön char responded to an increase in temperature by increasing their relative proportion of upstream movements, whereas Hornavan char responded in the opposite way. With the exception of March for Visjön char and April for Hornavan char, the respective response was more pronounced in fish fed reduced rations (Fig. 4).

The differential effects of increasing the water temperature are also reflected in the regression analysis (Table 1 A). A significant positive correlation between temperature and the percentage of movements directed upstream was recorded for Visjön char, whereas the correlation was significant and negative for Hornavan char. With the exception of Hornavan char fed surplus rations ($p=0.08$), these correlations were also significant for the separate experimental groups. The regression results also support the existence of a seasonal trend in rheotactic behaviour (Table 1 B).

Table 1. (A) Relation between temperature and percentage of movements directed upstream on a daily basis for Visjön and Hornavan Arctic char. Movements recorded under natural temperature conditions (February–June) and increasing temperature (February–May) for 10 days each month. Data pooled for both experimental groups of respective stock.

(B) Relation between season (day number) and percentage of movements directed upstream on a daily basis for Visjön and Hornavan Arctic char. Movements recorded during periods of increasing temperature during February–May for 10 days each month. Data pooled for both experimental groups of respective stock. r = coefficient of regression.

	Visjön char			Hornavan char		
	r	p	n	r	p	n
A	0.42	<0.001	180	−0.23	0.01	180
B	0.42	<0.001	80	−0.24	0.03	80

The correlation between day number and percentage of movements directed upstream during periods of increasing temperature, is significant for the two stocks. Again the association is positive for Visjön char and negative for Hornavan char.

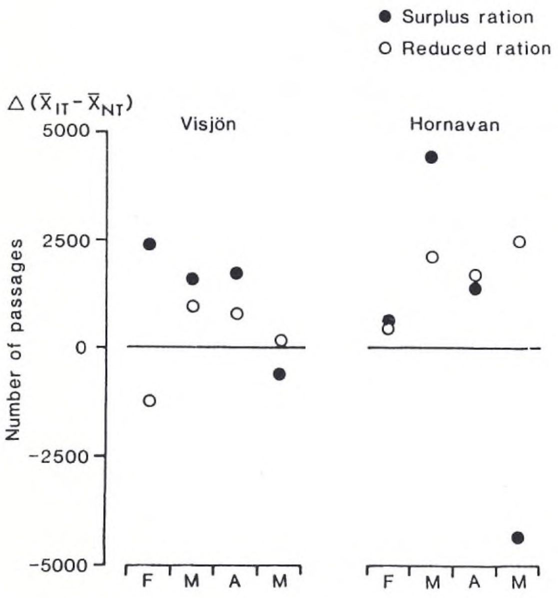

Figure 5. Effects of temperature on the total swimming activity of Visjön and Hornavan char, February–May 1987. Total activity (mean for 10 days) during a period of increasing temperature minus total activity (mean for 10 days) under natural temperature conditions within the same month.

For the separate experimental groups, significance is recorded only for Visjön char fed surplus rations.

Seasonal variation in total activity was relatively low, with Hornavan char generally being more active than Visjön char. Levels of total activity per day were, with a few exceptions, higher for periods with artificially increased temperatures than for the corresponding periods with natural temperatures (Fig. 5).

Discussion

The differences in rheotactic behaviour between Visjön and Hornavan char revealed in this study, may reflect genetic differences between these two Arctic char populations. No such differences have yet been reported in landlocked Arctic char. However, for several other salmonid species, differences in the rheotactic behaviour between populations have been demonstrated (Raleigh and Chapman 1971, Brannon 1972, Kelso and Northcote 1981, Kaya 1989).

It is evident that two-year-old Lake Visjön char clearly tended to favour upstream movements in June. This may be genetically influenced and an important part of the observed upstream migrations in the tributaries of Lake Visjön (Näslund 1991). During spring and early summer, juvenile char enter several creeks in an exploratory manner (Näslund 1991). Hornavan char, on the other hand, mainly swam downstream during this experiment. Downstream oriented swimming behaviour in two-year-old Hornavan char during spring and early summer has been documented previously by Schmitz (1991). She noted that the seasonal changes in seawater adaptability and migratory behaviour coincided with those of anadromous stocks, although Hornavan char have been isolated from the sea for about 6,000 years.

It also appeared as though the responses in my study were affected by the time of the year, i.e. the rheotactic responses were stronger in spring – early summer than during winter. Partly preprogrammed annual cycles have been demonstrated in growth potential for brown trout and

Arctic char (Brown 1945, Jobling 1987) and for smoltification in Atlantic salmon (*Salmo salar*) (Eriksson and Lundqvist 1982). There are also strong indications that certain aspects of the migratory behaviour of salmonids are preprogrammed (Eriksson 1975, Eriksson 1988). Thus, the changes in response during spring and early summer observed in this study may reflect the onset of a genetically determined period of exploratory behaviour in these juvenile char. In the field the upstream migration from Lake Visjön is confined to a period of two to three weeks during spring. It seems reasonable to assume that the seasonal timing of such migrations is determined by natural selection. Upstream migration during spring floods may increase the probability of gaining access to distant habitats. Moreover, it should be advantageous for the migrant to arrive and establish in the target habitat early in the season.

The fact that an increase in water temperature seemed to play an important role for the onset of upstream movements in Visjön char is in agreement with previous findings from Lake Visjön. Water temperature both initiated and guided the upstream migrations of juvenile char during spring (Näslund 1991). Emigration from Lake Visjön generally took place when the lake water temperature was lower than the temperature in the inflowing creeks. Upstream migration started at ambient creek temperatures as low as 2°C, but migration normally peaked at 6–8°C. The upstream swimming response recorded as a result of an artificially increased temperature in this experiment may very well have been lower than the potential response, since temperature was increased only 4–5°C from very low levels and over a relatively short period. The temperature increase and time required to initiate upstream swimming is not known for this population. But if a certain temperature is required for upstream migration, as reported for other salmonids (see Arnold 1974 for review), and if such a level had not been reached in this study, the resulting rheotactic response would probably have been weak.

Like char from Lake Visjön, Hornavan char also responded to increasing temperature, but by swimming downstream. Schmitz (1991) concluded that temperature initiated the negative rheotaxis observed in Hornavan char during spring. Keenleyside and Hoar (1954) registered a change from positive to negative rheotaxis in coho salmon (*Oncorhynchus kisutsch*) when the temperature was raised from 4–5°C to 13–14°C. Similarly, temperature has been identified as an important trigger of migratory behaviour in other studies on salmonids (Northcote 1962, 1969, 1984, Arnold 1974, Thorpe 1982, Smith 1985). In addition to initiating a rheotactic response, increasing temperature also resulted in a generally elevated level of activity in the experimental groups studied.

The results of this study also indicate that the response to water current initiated by temperature was somewhat stronger in fish fed reduced rations than in fish with a surplus food supply. Taken together, the results seem to be more consistent for fish fed reduced rations than for fish fed surplus rations. This is in agreement with the observation that first time migrants leaving Lake Visjön have a lower condition factor compared with non migratory fish of the same size (Näslund 1991). Food availability and condition are likely to reflect a fish's competitive ability, which in turn may be an important factor influencing migratory behaviour. Such a conclusion gain support in the literature. Slaney and Northcote (1974) pointed out that feeding conditions and migratory behaviour were related in young rainbow trout. Likewise, Nordeng (1983) showed that the number of migrants in an anadromous Arctic char population decreased as food levels were increased. Werner (1986) suggested that there is a direct relationship between competition and migration in fishes.

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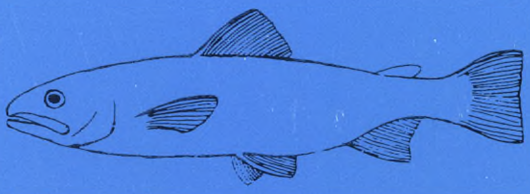

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