Ann. Zool. Fennici 33: 427–435 ISSN 0003-455X
Helsinki 28 November 1996

Growth and production of perch (*Perca fluviatilis* L.) responding to biomass removal

Arne Linløkken & Per Arne Holt Seeland

Linløkken, A., Hedmark College, Department of Agriculture and Natural Sciences, Blaestad, N-2322 Ridabu, Norway
Seeland, P. A. H., Ulvåbrua, N-2410 Hernes, Norway

Received 21 August 1995, accepted 12 December 1995

This study was carried out in the oligotrophic lake Munksjøen in South-East Norway. The lake is situated 569 m above sea level, its surface area is 48 ha and maximum depth 10 m. The fish fauna consists of perch, roach (*Rutilus rutilus* L.), pike (*Esox lucius* L.) and sparse populations of brown trout (*Salmo trutta* L.) and burbot (*Lota lota* L.). The water quality was poor due to acidification, with a pH level of about 5.0 until the summer of 1991 when 23 tonnes of limestone powder were added. Afterwards, pH > 6.0 was maintained, except for snowmelt periods when the pH dropped to 5.8. Liming was expected to improve recruitment, and to avoid overcrowding and stunting, the most numerous species, perch and roach, have been heavily fished with traps and gillnets annually since 1992. Density of the perch population was determined with the mark recapture experiment, and biomass and production in the period 1992–1994 were simulated by modelling. Biomass of perch was estimated to 9.5 kg/ha before the mass removal and to 2.8 kg/ha afterwards. The biomass reduction led to increased growth rate, and based on the model, 1–1.5 kg/ha of perch with a mean weight of 100 g may be caught annually.

1. Introduction

Perch (*Perca fluviatilis* L.) is known as an eastern invader in Norway because it entered the Norwegian river system through rivers running eastward to Sweden. Due to this, perch, like other eastern invaders, are abundant in southeastern, and also northeastern parts of the country (Huitfeldt-Kaas 1918). Perch is numerous in most lakes and tarns in the whole county of Hedmark, except for the mountain district in the northwest. Dense stunted populations of perch are usual, as in other areas (Alm 1946, LeCren 1958, Sumari 1971, Jensen 1976, Persson 1983, Rask & Arvola 1985).

The exploitation and consumption of perch has been negligible since the last war, even though traditions on perch fishery go back to the Stone Age. Bait fishery in summer and jigging in winter occur on a moderate scale.

In Munksjøen, a stunted population of perch was considered unattractive to local fishermen, and since the 1970s the lake has been influenced by acidifica-

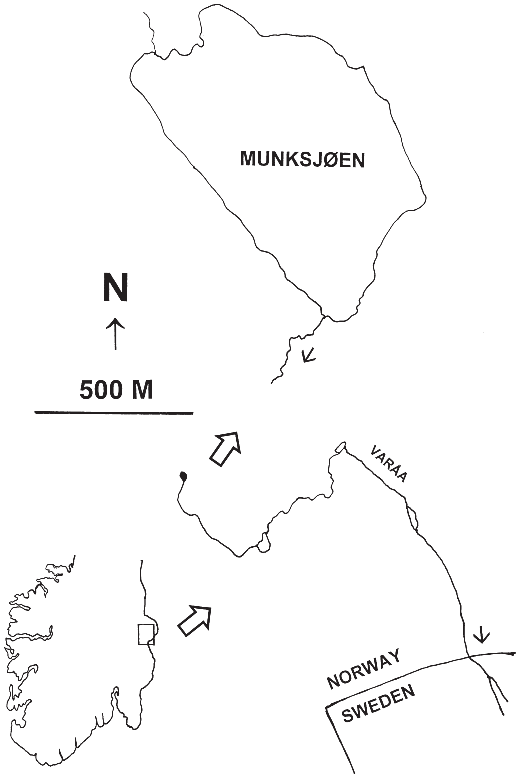

Fig. 1. Sketch map of the study locality.

tion like most other lakes of high altitudes in this area. To overcome this, the lake was limed in autumn 1991 and winter 1995, and heavy fishery was put on for all species present, and to depress recruitment, stocking with 1–4 year-old brown trout (*Salmo trutta* L.) was done in 1992–1994.

Roach (*Rutilus rutilus* L.) is the most numerous species beside perch in Munksjøen. Perch and roach compete for nutrition but the roach is probably the most effective, especially at the young stage when both feed on zooplankton (Persson 1986, Persson & Greenberg 1990), though roach seems less superior in oligotrophic water (Persson *et al.* 1991, Bergman & Greenberg 1994). Pike (*Esox lucius* L.) predates on both species but prefers roach or other cyprinids to perch (Mauck & Coble 1971, Robinson 1989).

To assess the effects of the liming and mass removal, a survey program was followed to answer the following questions: 1) What is the biomass of perch in the lake? 2) What manual effort with traps and gillnets is necessary to increase growth of perch by mass removal? And 3) How much perch of an "acceptable size" may be produced and harvested in the lake?

2. Materials and methods

2.1. The study lake

Munksjøen (569 m a.s.l.) is situated in South-East Norway and drains to River Varåa, which is again drained by River Klara and Lake Vänern in Sweden (Fig. 1). The surface area is 48.2 ha, mean depth 3 m, maximum depth 10 m, the catchment is 4.47 km^2 and the retention time is 1.9 years. Boggy moorland with coniferous trees dominates the catchment, and the lake is oligotrophic to dystrophic, and has during the last decades been exposed to acidification like most of the elevated lakes in this area (Rognerud 1992). In summer 1991, 23 tonnes of limestone powder was added, and the treatment was repeated with 30 tonnes in winter 1995. Water samples were analysed for six parameters and the maximum values of pH, alkalinity and Ca were recorded after liming: pH = 4.98–6.64, conductivity 1.5–1.8 mS/m, colour 62–95 mg Pt/l, alkalinity = 11–83 mekv./l, 1.7–2.9 mg Ca/l, 13–29 mg/l monomeric aluminium, less than 10 mg/l was labile form (Driscoll *et al.* 1980), which is very low.

The fish fauna in Munksjøen consists of five species; perch, roach, pike, a very sparse population of burbot (*Lota lota* L.), and brown trout was practically extinct when the investigations began in 1992. Populations of perch and roach were dense before acidification, and exploitation has been negligible during the last decades.

The population of brown trout was sparse for several reasons: limited spawning areas, acidification and predation from pike. Stocking of artificially-reared brown trout has been carried out as follows: 650 two-year-old specimens in autumn 1991, and 1 700 one-year-old, 800 two-year-old and 170 four-year-old specimens in 1992.

2.2. Population estimates

Perch females mature from age 4 and in the following perch older than 4 years are referred to as adult perch. Adult perch were caught in traps and marked by finclipping, and density was estimated by Schnabel's (1938) method (cited in Ricker 1975) at the end of fishing in June 1993 (N_{1993}) and at the beginning of fishing in May 1994 (N_{1994}). Computation of confidence limits was based on the assumption that recaptures R were Poisson distributed (Ricker 1975).

2.3. Catch and effort

Test fishing was carried out in May 1992, May–June 1993, 1994, and 1995. Two types of survey nets were used. One consisted of 8, 1.5 × 25 m, nets with different mesh sizes

(12.5, 16.5, 19.5, 21, 24, 26, 29 and 35 mm), and another, multimeshed "Nordic survey net" consisted of short, 1.5 × 2.5 m, segments of 12 mesh sizes (5, 6.25, 8, 10, 12.5, 16, 19.5, 24, 29, 35, 43 and 55 mm). The nets were set from the shore, towards the deep. The mass removal was done by heavy fishing with wire net traps (12.5 mm mesh size) and gillnets of both the survey series, and by single nets (1.5 × 25 m) of meshes 21, 22.5 and 24 mm. The effort with 12.5–24 mm gillnets in square metres of net surface was 250 m^2/ha in 1992, 2.7 m^2/ha in 1993, 6.6 m^2/ha in 1994 and 3.1 m^2/ha in 1995. The effort on trap nights was 5.0/ha in 1992, 26/ha in 1993 and 18/ha in 1994. From the beginning of June, bread was used as bait in the traps to attract both perch and roach.

2.4. Analysis and calculations

Age was determined by otoliths and operculum (Linløkken *et al*. 1991, Kleiven unpubl.). Otoliths were burned and cracked, after which the cross section was studied under a microscope. Back calculation of growth was based on operculum (LeCren 1947). A regression model of operculum radius (B, mm) on natural fish length (L, mm) was found:

$$\log B = 1.0226 \log L - 1.343 \quad (1)$$
$$(r = 0.9774,\ n = 205,\ p < 0.001).$$

Regressions of fish weight (W, g) on fish length (L, mm) was determined for each year and were used to calculate the condition factor K:

$$\log W = b\log L + \log a \ \text{ or } \ W = aL^b \quad (2)$$

$$K = a \times 10^5 \times L^{b-3} \quad (3)$$

The weight on length regressions were also used to estimate fish weight in previous years, which in turn were used to calculate instantaneuos growth rates $G = \ln(W_2/W_1)$ (Ricker 1975), where W_2 is the mean weight in the actual year, and W_1 is the mean weight the year before. Weights of mature females were adjusted for the ripe ovaries by assuming that spent female gonads contributed 1.5% of somatic weight, which was the mean value calculated from females caught after spawning. Immature females were only found among younger year classes whose length distribution did not overlap with that of the mature fish. To attain smooth curves of G on age, regression models of log$G$ on age were determined from the materials from all years, describing the growth rates in the population the year before. Stomach contents of perch and brown trout were examined for fish remains.

Survival rate (S) during a particular period of time is calculated by comparing the estimated number of perch (N_1) at the beginning of the period and the number of perch at the end of the period (N_2): $S = N_2/N_1$, and then instantaneous mortality rate $Z = -\ln S = M + F$, where M is instantaneous mortality by natural causes and F is the instantaneous mortality caused by fishing. Fishing was done during one month and natural mortality was considered as zero, compared with fishing mortality during that time. Survival of adult perch during fishing (S_F) in 1993 can be calculated by $S_F = e^{-F} = N_{1993}/(N_{1993} + C)$, where C is the number of perch caught in 1993, and N_{1993} is the number of perch after fishing. Survival for the rest of the year (S_M), when only natural mortality was applicable, can be calculated by $S_M = e^{-M} = N_{1994}/N_{1993}$, where N_{1994} is the number of perch before fishing in 1994, and then $F = -\ln S_F$ and $M = -\ln S_M$. Yield (Y) is calculated as $Y = C \times w$ (w = mean weight) or $Y = F \times B_M$ (B_M = mean biomass during the fishing period). The mean biomass (B_M) during a period with mortality Z is found by $B_M = B_0 \times e^{-(Z/2)}$, where B_0 is the biomass at the beginning of the period. By assuming no natural mortality, compared with fishing mortality during fishing, $Z/2 = F/2$. G is used to estimate production $P = B_M \times (G - Z)$ (Ricker 1975).

Estimated stock and mortality rates were used to simulate stock number, biomass, yield and production of adult perch for year classes born before 1988, in all years 1992–1994, by iterations on an Excel worksheet with models described by Ricker (1975). Net production during the first 4 years of a cohort's lifetime was considered as the biomass of 4-year-old perch.

Recruitment of perch has been correlated to temperature (Neuman 1976, Koonce *et al*. 1977, LeCren *et al*. 1977) so monthly average air temperatures in May and June each year during the period 1980–1994, recorded from the Norwegian Metereological Institute, were compared with the average for these months for the whole period to reveal a possible correlation.

3. Results

3.1. Density and mass removal

Schnabel's estimate gave 3 185 perch at the end of fishing in 1993 and 2 643 at the beginning of fishing in 1994, corresponding to 2.8 and 2.7 kg/ha (Table 1). Perch contributed 40% of weight caught in survey nets in 1992, reducing to 14% in 1994, and increasing again to 43% in 1995 (Fig. 2). The fraction of roach varied between 21 and 79%, the highest being

Table 1. Stock assessments of perch in Munksjøen in 1993 and 1994, based on mark and recapture (M = number marked, C = number caught, R = number recaptured, N = number estimated).

	1993	1994
$M \times C$	146 874	124 242
R	28	47
N	3 185	2 643
95% *c.l.*	2 286–4 966	1 988–3 601
Mean weight, g	42	49
Biomass, kg	134	130
Biomass, kg/ha	2.8	2.7

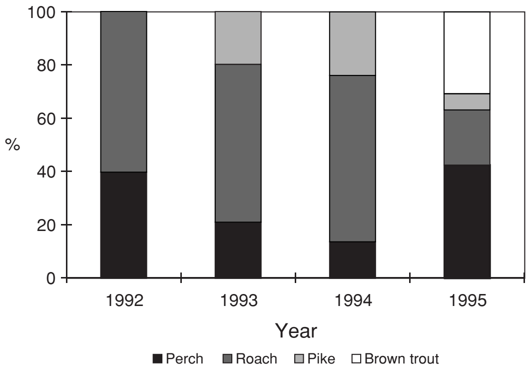

Fig. 2. Species composition by weight in the survey net catches.

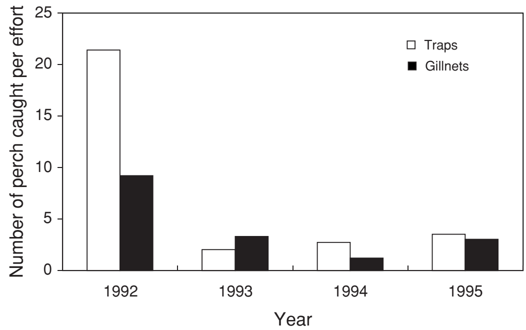

Fig. 3. Number of perch caught per unit effort (*CPUE*) with wirenet traps and gillnets; meshes 12.5–24 mm.

in 1993 and the lowest in 1995. The fraction of brown trout was high in 1995 but that was partly caused by a 1.2 kg specimen. The removal in 1992 of 773 kg of fish, mostly perch and roach, corresponds to a harvest of 16.0 kg/ha (Table 2). Roach had the highest fraction of biomass removed from the lake in 1992 and 1994, whereas perch had the highest fraction in 1993. The fraction of perch catches taken by traps were: 50% in 1992, 99.5% in 1993 and 84% in 1994. The increasing fraction caught in traps after 1992 was because the gillnet effort was lowered to spare the stocked brown trout. The fraction of roach catches taken by traps were: 2.5% in 1992, 92% in 1993 and 9% in 1994. The high fraction caught in traps in 1993 was partly due to the reduced gillnetting, but was also due to the use of bait in the traps after spawning.

The mean weight of perch increased from 29 g in 1992 to 49 g in 1994, and decreased again to 33 g in 1995. The mean weight of roach also increased from 1992 to 1994, and decreased in 1995, and that of pike was highest in 1992, and was heavily reduced in 1993. From 1994, when a special effort was made for pike by fyke nets, both harvest and mean weight increased. The fraction of pike in the catches peaked in 1995 with 44.8 kg or 67% of the total 66.7 kg that year. The fraction of brown trout increased during the period, and so did the mean weight.

3.2. Mortality

Based on catches of perch and estimated stock, the fishing mortality in 1993 was:

$$F_{1993} = -\ln S_F = -\ln[N_{1993}/(N_{1993} + C_{1993})] = 0.57.$$

Survival from the end of fishing in 1993 to stock assessment at the beginning of fishing in 1994 was estimated by $S_M = N_{1994}/N_{1993} = 0.83$ and $M = -\ln S_M = 0.19$ for approximately eleven months, which means an annual $M = 0.21$. According to the model, the number of perch recruited in the catches before 1992, decreased from 16 400 in 1992 to 1 181 in 1995 (Table 3), corresponding to 459 kg or 9.5 kg/ha in 1992, and 70 kg or 1.5 kg/ha in 1995. That is a 84% reduction. The biomass

Table 2. Species composition in weight (*Y*, kg) and mean weight (*w*, g) of the fish in the yearly total survey catches of Munksjøen in 1992–1995.

	1992		1993		1994		1995	
	Y	*w*	*Y*	*w*	*Y*	*w*	*Y*	*w*
Perch	286.4	29	102.5	43	52.7	49	19.1	33
Roach	445.2	58	18.8	52	83.7	76	1.3	29
Pike	41.1	955	7.4	151	27.7	322	44.8	487
Burbot	0.15	75		–	0.3	150		
Brown trout	0.10	50		–	1.0	250	1.5	375
Total harvest, kg	773.0		128.7		165.4		66.7	
Harvest, kg/ha	16.0		2.7		3.4		1.4	

may be expected to increase in 1995 due to increased growth rate and a low mortality rate.

3.3. Catch per unit effort

The catch per unit (10 m^2/night) effort (*CPUE*) in the meshes 12.5, 16, 19.5, 21 and 24 mm (Fig. 3) was correlated to modelled stock size (N) at the beginning of fishing each year 1992–1995:

$$CPUE = 5.62 \times 10^{-4} \times N - 0.00124 \quad (4)$$
$$(r = 0.999, n = 4, p < 0.001).$$

This may be transformed to N/ha = 36.9 × *CPUE*, or N/ha ≈ 20 × C/(series of Nordic survey nets) when only the five meshes 12.5–24 mm are included. The catch per effort in traps, showed less correlation as the catches were very high in the first year, 21 perch per trap night, compared with less than 3 and no correlation to density the other years. The trap fishery in 1992 was more restricted to the spawning period of perch.

3.4. Manual effort

One person may handle net catches of about 500 perch per day. The gill net effort necessary to catch that number may be calculated using equation (4). A skilled person may handle and empty 15 traps an hour, and the total effort in 1992 was 242 trap nights, or 2–3 normal working days.

3.5. Recruitment

The age distributions of perch indicate recruitment failure from 1985 to 1990, but recruitment was improved in 1991, and especially in 1992 (Fig. 4). In 1992, 47% of the catches were perch of the 1984 year class, whereas in 1995, 45% of the catches were of the 1992 year class. Air temperature in May was 11.2°C in 1992, compared with 8.9°C on average during 1980–1993, and 15.1°C compared with 13.2°C on average in June. The air temperature also exceeded the average with 1°C in May 1984.

3.6. Growth

The growth of perch declined at 15–17 cm before 1992 (Fig. 5). After the mass removal from 1992, the growth increased considerably. Before 1992, perch exceeded 15 cm after 6–7 years, whereas in 1995, 4–5-year-old perch exceeded 15 cm, and perch older than 5 years exceeded 20 cm. On the other hand, three-year-old perch of the new strong year class showed only moderate growth. There was also an increase in the condition factor of

Table 3. Number of perch according to Schnabel estimate (N_E) and according to model (N_M), instantaneous natural mortality (M) based on N_E, and instantaneous mortality caused by fishery based on N_E and observed catches (C_O). C_M are the catches simulated by mean N_M and F. w = mean weight (g) in the catches and B (kg) and Y (kg) is biomass and yield. (f = fishing).

Year		N_E	N_M	M	F	C_O	C_M	w	B	Y
	Before f		16 400						459	
1992	During f		10 510		0.89	9 363	9 353	28	294	262
	After f		6 735	0.19						
	Before f		5 569						234	
1993	During f		4 188		0.57	2423	2417	42	176	100
	After f	3 185	3 118	0.19						
	Before f	2 643	2 604						128	
1994	During f		1 929		0.60	1183	1146	49	95	58
	After f		1 429	0.19						
	Before f		1 181						70	
1995	During f		1 152		0.05	55	57	60	68	3.4
	After f		1 123	0.19						

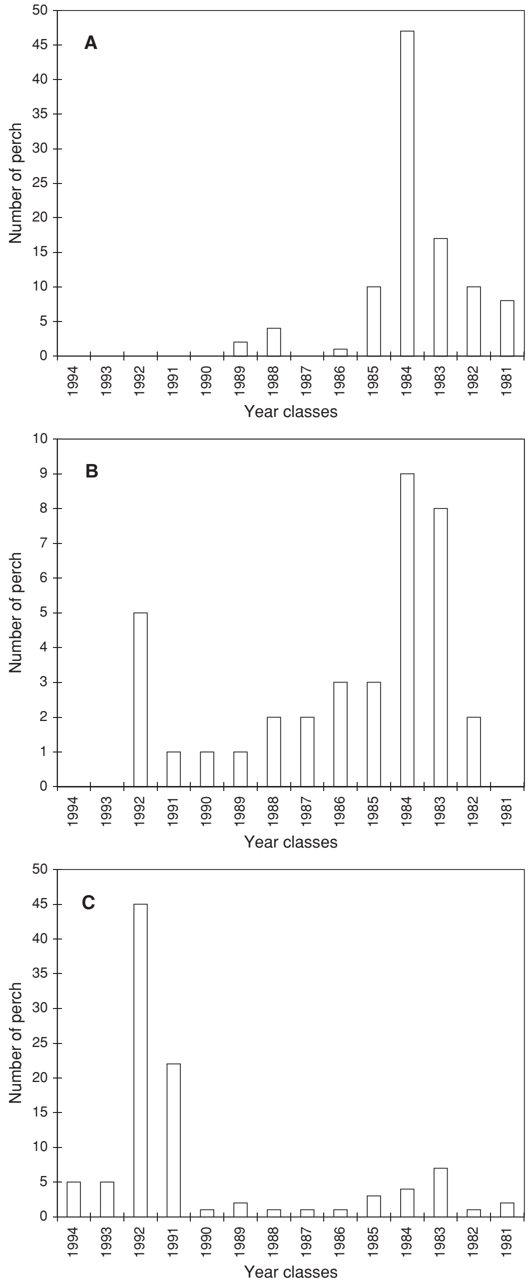

Fig. 4. Age distribution of perch caught in survey nets: — A: in 1992 (N = 97). — B in 1994 (N = 37). — C in 1995 (N = 100).

15 cm long perch from K = 0.85 in 1992 to 0.90 and 1.0 in 1994 and 1995, respectively (Table 4). The instantaneous growth rate (G), relative to age, increased considerably from 1992 to 1994 (Fig. 6).

3.7. Piscivory

In July 1992, 20 specimen of old perch were examined, and 16 of them had one or more perch fry in the stomach. In July 1995, four of 12 examined perch > 20 cm had remains of 1–2-year-old perch or roach in the stomach. The 1.2-kg brown trout had two 10-cm-long roaches in the stomach.

3.8. Biomass, production and yield

The biomass, production and yield, according to modelling, was based on the following assumptions: If roach is heavily reduced, the growth rate (G) recorded in 1995 (the 1994 season), may be maintained with a biomass of 200 kg of adult perch. G recorded in 1994, will be maintained at a biomass of 400 kg, whereas G from 1992 is maintained at a biomass of 800 kg.

Only a biomass of 200 kg of adult perch, or 4 kg/ha, will give catches with a mean weight above 100 g (Fig. 7). If perch is recruited to the catches at age 6, instead of 5, the mean weight will increase from 100 to 110 g, whereas the yield will increase from 61 to 63 kg. The highest yield is attained with the highest density, but the mean weight will be below 20 g. The yield and production of adult perch is approximately equal in the four different cases, which means that the whole net production of perch must be caught to attain the predicted yield. The relationship P/B of adult perch was calculated as 0.11 at biomass 800 kg, and 0.18 at biomass 200–400 kg.

4. Discussion

Munksjøen had a low biomass of fish even in 1992; before the mass removal, 336 specimens/ha or 9.5 kg/ha of perch and a total fish biomass of approximately 24 kg/ha. Other investigations in Norway have come up with 573 specimens/ha (Jensen 1976) and 441–932 specimens/ha, corresponding to 70–90 kg/ha (Kjellberg 1994). Rask and Arvola (1985) reported 1 240–2 700 perch/ha, corresponding to 19.0–38.0 kg/ha, among a total fish biomass of 32–40.5 kg/ha in two slightly acidified small lakes. The presence of roach is probably, at least partly, responsible for the low density of perch. Sumari (1971) found average perch biomass of 8–9 kg/ha

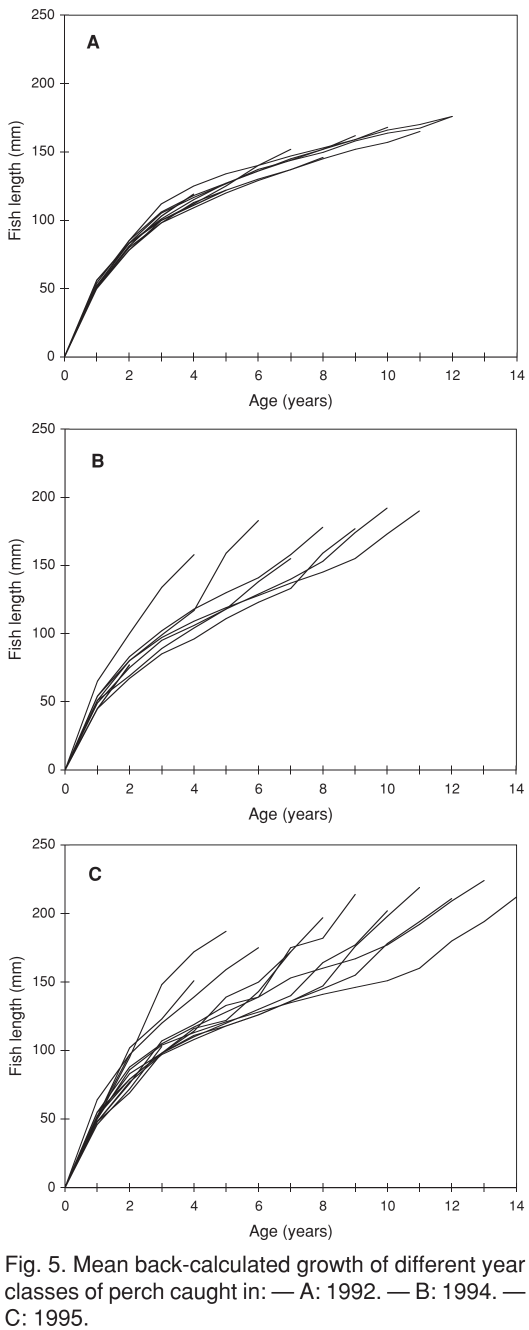

Fig. 5. Mean back-calculated growth of different year classes of perch caught in: — A: 1992. — B: 1994. — C: 1995.

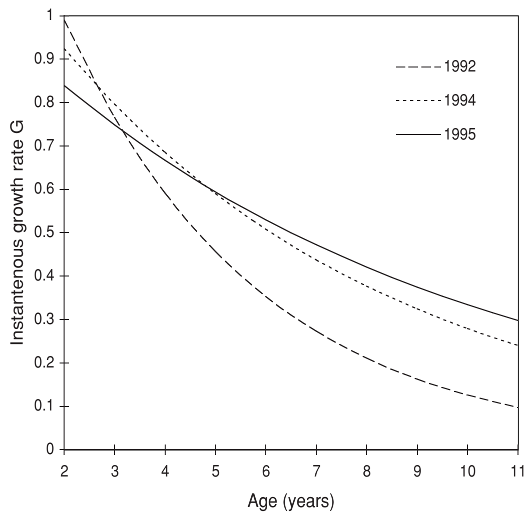

Fig. 6. Regression curves of log$G$ on age for perch caught in 1992, 1994 and 1995.

in lakes with competitors. Lappalainen *et al.* (1988) reported 6–261 perch/ha, corresponding to 1–13.5 kg/ha in acidified lakes in Finland, compared with 1 432–3 358 perch/ha or 19.5–51.7 kg/ha in two reference lakes.

Age distribution of perch showed recruitment failure during 1985–1990, probably due to acidification. Recruitment of perch may be depressed by predation from old perch if abundance is sufficient (Alm 1946, Craig & Kipling 1983), but that is unlikely with the low density in Munksjøen. The improvement in 1991 occurred the same year as the lime treatment, but the lime treatment took place two and a half months after hatching, which makes it difficult to connect it to effects of the liming, as the hatching stage is assumed to be the most critical (Mount 1973, Haines 1981, Magnusson *et al.* 1984, Lappalainen *et al.* 1988). The low density of adults, combined with improved water quality and high temperature in May–July in 1992, resulted in strong recruitment that year.

As Munksjøen is an oligotrophic lake on a relatively high latitude, slow growth was to be expected.

Table 4. Length-weight relationships, number of specimens, regression coefficient r and condition factor K of 15-cm-long perch from Munksjøen in 1992, 1994 and 1995.

1992	$W = 1.06 \times 10^{-5} \times L^{2.955}$	$N = 97$	$r = 0.953$	$p < 0.001$	$K = 0.85$
1994	$W = 3.32 \times 10^{-6} \times L^{3.199}$	$N = 37$	$r = 0.994$	$p < 0.001$	$K = 0.90$
1995	$W = 4.84 \times 10^{-6} \times L^{3.151}$	$N = 100$	$r = 0.993$	$p < 0.001$	$K = 1.03$

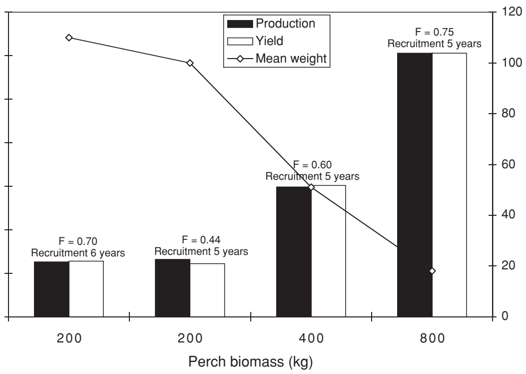

Fig. 7. Simulated production, yield and mean weights in the catches of perch older than 4 years, based on assumptions of growth rates at three different biomass levels.

Reduction of the perch stock from 9.8 kg/ha in 1992 to 2.7 kg/ha in 1994, increased the growth rate, both by length and condition as LeCren (1958) reported from Windermere. Though the fish density was low, even before the mass removal, the growth was slow. During 1985–1990 the density must have been reduced gradually, due to natural mortality and a minor recruitment, but back-calculated growth in 1992 did not show any obvious increase. Lappalainen *et al*. (1988), Raitaniemi *et al*. (1988) and Linløkken *et al*. (1991) compared growth of perch from lakes of different stages of acidification and found improved growth in the most acidified lakes. Physiological stress and reduced production of nutritional organisms may have counteracted a growth response in Munksjøen. The growth response after 1992 may, therefore, partly be caused by the water quality improvement, and not only by the mass removal. Ryan and Harvey (1980) found increased growth of young yellow perch (*Perca flavescens* M.), but reduced growth appeared at about 14 cm compared with perch in water with a higher pH, and that corresponds to the perch in Munksjøen. The moderate growth of the strong 1992 year class of perch indicates increased competition again in that cohort, and the fact that the growth of adult perch still was enhanced, indicates that competition between adult perch and the younger ones is minor.

The 1992 year class, therefore, must be monitored and a sufficient proportion should be removed during 1996 to avoid overcrowding. It is impossible to predict the effort necessary to attain a suitable recruitment, but it will most probably be less than the effort spent in 1992. If the biomass of adult perch is kept at 4–5 kg/ha and roach is kept at a minimum, the mean weight in the perch catches probably will remain at about 100 g, and ca. 60 kg or 1–1.5 kg/ha may be harvested. Persson (1986) managed to increase perch biomass by 140% by reducing roach to a minimum. It is possible that a low fish density over several years may lead to increased biomass of nutrition organisms like insect larvae, and faster growth may increase the fraction of piscivorous specimens. In that case, the growth rate may increase further and remain high at a higher biomass than predicted. Another strategy of management in Munksjøen is to continue the stocking of big hatchery-reared brown trout, which eats both roach and perch. However, that would be expensive and the fishable stock would be sparse.

Assuming a mean biomass of 200 kg of adult perch in Munksjøen, a mean weight of 100 g and a yield of 60 kg per year, the correlation between *CPUE* and number of perch may be transformed to weight: Y (kg) per 10 m^2 of gillnet a night $= 5.6 \times 10^{-4} \times 200$ kg $= 0.112$ kg. To catch 60 kg, 5 360 m^2 of gillnet a night (111 m^2/ha) or 143 nets of the 1.5×25-m nets would be necessary. That will be somewhat less than half of the gillnet effort in 1992, when 250 m^2 gillnet/ha was used.

Acknowledgements. We thank Arne Nohr and Nils Myrene, chairmen of the Osensjøen Fishing Committee, and also Tore Qvenild at the Hedmark Environmental Administration for his enthusiasm and support during our work.

References

Alm, G. 1946: Reasons for occurrence of stunted fish populations with special regard to perch. — Rep. Inst. Freshw. Res. Drottningholm 25: 1–146.

Bergman, E. & Greenberg, L. A. 1994: Competition between a planktivore, a benthivore, and a species with ontogenetic diet shifts. — Ecology 75: 1233–1245.

Craig, J. F. & Kipling, C. 1983: Reproduction effort versus environment, case histories of Windermere perch and pike. — J. Fish Biol. 22: 713–727.

Driscoll, C. T., Baker, J. P., Bisogni, J. & Schofield, C. I. 1980: Effects of aluminium speciation on fish in dilute, acidified waters. — Nature 284: 161–164.

Haines, T. A. 1981: Acid precipitation and its consequences for aquatic ecosystems: a review. — Trans. Am. Fish.

Soc. 110: 669–707.
Huitfeldt–Kaas, H. 1918: Ferskvandsfiskenes utbredelse og innvandring i Norge, med et tillæg om kebsen. — Centratrykkeriet, Kristiania.
Jensen, K. W. 1976: Estimates of a population of spawning perch and of the efficiency of trap and gill-net fishing. — Rep. Inst. Freshw. Res. Drottningholm 55: 45–50.
Kjellberg, G. 1994: Fishery biological investigations in three watersheds in Rødsmoen 1993. — Norwegian Institute of Water Research. Report 0-93107. 45 pp.
Koonce, J. F., Bagenal, T. B., Carline, R. F., Hokanson, K. E. F. & Nagiec, M. 1977: Factors influencing year-class strength of percids: A summary and a model of temperature effects. — J. Fish. Res. Board Can. 34: 1900–1908.
Lappalainen, A., Rask, M. & Vuorinen, P. J. 1988: Acidification affects the perch populations in small lakes of southern Finland. — Env. Biol. Fish. 21: 231–239.
LeCren, E. D. 1947: The determination of the age and growth of perch (Perca fluviatilis) from the opercular bone. — J. Anim. Ecol. 16: 188–204.
— 1958: Observations on the growth of perch over twenty-two years with special reference to the effects of temperature and changes in population density. — J. Anim. Ecol. 27: 287–334.
LeCren, E. D., Kipling, C. & McCormack, J. C. 1977: A study of the numbers, biomass and year-class strengths of perch in Windermere from 1941 to 1966. — J. Anim. Ecol. 46: 281–307.
Linløkken, A., Kleiven, E. & Matzow, D. 1991: Population structure, growth and fecundity of perch in an acidified river system in southern Norway. — Hydrobiologia. 220: 179–188.
Magnuson, J. J., Baker, J. P. & Rahel, F. J. 1984: A critical assessment of effects of acidification on fisheries in North America. — Phil. Trans. R. Soc. Lond. B 305: 501–516.
Mauck, W. L. & Coble, D. W. 1971: Vulnerability of some fishes to northern pike predation. — J. Fish. Res. Board Can. 28: 957–969.
Mount, D. 1973: Chronic effect of low pH on fathead minnow survival, growth and reproduction. — Water Res. 7: 987–983.
Neuman, E. 1976: The growth and year-class strength of perch in some Baltic archipelagoes, with special reference to temperature. — Rep. Inst. Freshw. Res. Drottningholm 55: 51–70.
Persson, L. 1983: Food consumption and competition between age classes in a perch population in a shallow eutrophic lake. — Oikos 40: 197–207.
— 1986: Effects of reduced interspecific competition on resource utilization in perch. — Ecology 67: 355–364.
Persson, L. & Greenberg, L. A. 1990: Juvenile competitive bottlenecks: the perch-roach interaction. — Ecology 71: 44–56.
Persson, L., Diehl, S., Johansson, L., Andersson, G. & Hamrin, S. F. 1991: Shifts in fish communities along the productivity gradient of temperate lakes: patterns and importance of size-structured interactions. — J. Fish Biol. 38: 281–293.
Raitaniemi, J., Rask, M. & Vuorinen, P. J. 1988: The growth of perch in small lakes at different stages of acidification. — Ann. Zool. Fennici 25: 209–219.
Rask, M. & Arvola, L. 1985: The biomass and production of pike, perch and whitefish in two small lakes in southern Finland. — Ann. Zool. Fennici 22: 129–136.
Ricker, W. E. 1975: Computation and interpretation of biological statistics of fish populations. — Bull. Fish. Res. Can. 382 pp.
Robinson, C. L. K. 1989: Laboratory survival of four prey in the presence of northern pike. — Can. J. Zool. 67: 418–420.
Rognerud, S. 1992: (Water quality survey in Hedmark county. A regional survey of 220 lakes in 1988). — Environmental Administration. County of Hedmark. 30 pp. (In Norwegian.)
Ryan, P. M. & Harvey, H. H. 1980: Growth responses of yellow perch to lake acidification in the La Cloche Mountain lakes of Ontario. — Env. Biol. Fish. 5: 97–108.
Schnabel, Z. E. 1938: The estimation of the total fish population of a lake. — Am. Math. Mon. 45: 348–352.
Sumari, O. 1971: Structure of the perch populations of some pounds in Finland. — Ann. Zool. Fennici 8: 406–421.