

Recovery of acidified lakes in Finland and subsequent responses of perch and roach populations

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Finnish lake survey and Finnish fish-status survey indicated that 4900 small headwater lakes suffered from acidic deposition and 1600–3200 roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) populations were affected or extinct by the end of 1980s. Since the late 1980s, successful sulphur emission reductions in Europe have induced a chemical recovery of acidified lakes. This resulted in decreases in sulphate and labile aluminium concentrations and increases in pH and alkalinity during the 1990s. The first signs of recovery in affected perch populations were observed in the early 1990s. New strong year-classes appeared and the population structure returned to normal. Little if any recovery of the affected populations of the more acid-sensitive species, roach, was recorded. This may have been due to still critical water quality conditions for successful reproduction of sensitive roach and/or organic acid episodes in the 2000s, suppressing the recovery of buffering capacity.

Introduction

The multidisciplinary Finnish Acidification Research Programme (HAPRO) in 1985–1990 revealed that a considerable number of small headwater lakes (lake area 0.01–1 km²) in Finland were suffering from acidification and damage to fish populations. In connection with HAPRO, the lake status survey in 1987 estimated the number of acidic (Gran alkalinity $\leq 0 \mu\text{eq l}^{-1}$) lakes to be 4900 (Forsius *et al.* 1990). Correspondingly, a fish status survey in

1985–1987 reported declines and also extinctions of sensitive fish species in small lakes due to anthropogenic acidification in southern and central Finland (Rask and Tuunainen 1990). Based on the fish-status survey of 80 lakes (Rask and Tuunainen 1990) and modelling of water chemistry data from 783 statistically selected lakes (Forsius *et al.* 1990), the number of lakes in southern and central Finland in which fish populations were estimated to be affected due to acidification, was 2200–4400, and out of these 1000–2000 fish populations were estimated to be

lost (Rask *et al.* 1995a). The most damaged were the populations of roach, and to a lesser extent European perch, the most common species in small lakes in southern and central Finland. The fish status survey of Finnish lakes (lake area ≥ 0.04 km²), based on postal inquiries, in connection with the Northern European Lake Survey in 1995 (Henriksen *et al.* 1998), suggested somewhat lower impacts with ca. 700 fish populations lost and 1200 affected, and these were almost all roach populations (Tammi *et al.* 2003). Both surveys suggested that perch was not extinct in any of the lakes. However, outside the coverage of these surveys based on statistical sampling of lakes (Forsius *et al.* 1990, Tammi *et al.* 2003), some lost perch populations were documented in strongly acidified lakes (Rask and Tuunainen 1990, Nyberg *et al.* 2010).

Sulphate deposition has been the major driving force to the anthropogenic acidification of surface waters in Finland as well as in other Nordic Countries (Skjelkvåle *et al.* 2001) and elsewhere in Europe (e.g. Prechtel *et al.* 2001, Wright *et al.* 2005). Following the general decreasing trend in sulphate deposition in Finland since the late 1980s (e.g. Vuorenmaa 2004), the regional recovery of acid sensitive Finnish lakes, indicated by decreasing concentrations of sulphate and increasing alkalinity, was first observed in the early 1990s (Mannio and Vuorenmaa 1995). At the same time, the first signs of recovery in affected perch populations were recorded (Nyberg *et al.* 1995, Rask *et al.* 1995b). The recovery of lakes from acidification has been most evident in southern Finland, where lakes were both exposed to the highest sulphate deposition and showed the strongest responses to emission reduction (Vuorenmaa 2004, Vuorenmaa and Forsius 2008). Sulphur deposition in southern Finland has declined by about 60%–70% since the late 1980s (Vuorenmaa 2007). Nitrogen deposition has also decreased, but less than that of sulphur, by about 30%–40% since the late 1980s (Vuorenmaa 2007, Ruoho-Airola *et al.* 2014).

In this study, we present patterns in water quality recovery from acidification and subsequent responses of perch and roach populations in selected acid-sensitive monitoring lakes of southern Finland during a 25 year period, 1985–2009. Because the period of our study covers the years

of strongest acidification pressure on lakes, we had the opportunity to record the decline of fish populations, some of which became extinct. Further, after the onset of the chemical recovery of the lakes, we could detect the start and follow the progress of the recovery of fish populations, including changes in fish abundance and growth. Attention was also paid to a comparison in responses of an acid tolerant (perch) and a sensitive (roach) species, including the potential effects of increased organic carbon concentrations on the two species in the later part of the study period.

Material and methods

The lakes

Finnish Game and Fisheries Research Institute and Finnish Environment Institute started an integrated monitoring of water chemistry and fish populations in acidified lakes in the early 1990s (Rask *et al.* 1995b). Twelve of these lakes, examined since the Finnish Acidification Research Programme (HAPRO) in 1985–1990, were included in the present study. They represent the following four levels (three study lakes in each level) of fish community response to acidification in small Finnish lakes according to Rask *et al.* (1995a): (1) perch extinct (pH < 5; Al_{lab} 80–280 $\mu\text{g l}^{-1}$), (2) perch affected (pH 4.8–5.5; Al_{lab} 50–160 $\mu\text{g l}^{-1}$), (3) roach extinct (pH 5.2–6.0; Al_{lab} 25–135 $\mu\text{g l}^{-1}$), and (4) roach affected (pH 5.3–6.4; Al_{lab} 5–40 $\mu\text{g l}^{-1}$).

In lake group 1 “perch extinct”, according to sediment diatom analyses rapid acidification took place in the 1960s (Tolonen and Jaakkola 1983, Tulonen 1985). In lake group 2 “perch affected”, rapid acidification started in the 1950s in Munajärvi (Tolonen *et al.* 1986) and in the 1960s in Orajärvi (Tolonen and Jaakkola 1983). In group 3 “roach extinct”, no paleolimnological records on the acidification history are available, but according to calculations on pre-acidification alkalinity (Kämäri 1985), these lakes were also acidified. In Kattilajärvi of group 4, a half pH unit decrease to the level of 5.5 was set to the 1960s (Liukkonen 1989).

Moreover, according to information from local people, the first disappearances of roach

populations had occurred as early as during the 1950s in some small lakes of an acid-sensitive upland forest area in southernmost Finland, including Iso Lehmälampi in group 1 (Rask and Tuunainen 1990).

Water quality

The water chemistry samples were taken from the middle of each lake, commonly once a year during the autumn overturn phase. This autumnal sampling strategy is considered representative for long-term monitoring of conservative acidification ions (Mannio 2001a, 2001b). Lakes Iso Lehmälampi, Vitsjön and Kattilajärvi have been more intensively monitored from the early 1990s, and in these lakes seasonal sampling strategy has been applied: one sample during the winter stratification, two samples during the spring flows, one sample during summer stratification and two samples during the autumn overturn. The chemical analyses were carried out by the laboratory of the Finnish Environment Institute according to the standardized methods described thoroughly by Forsius *et al.* (1990) and by Vuorenmaa (2007). In this study, the main emphasis is on parameters reflecting changes in acidification status and chemical recovery: alkalinity (Gran method) and pH, charge-balance ANC (ANC_{CB}), non-marine sulphate (xSO_4), non-marine base cations $xBC = (xCa + xMg + xNa + xK)$, labile Al, NO_3 -N and total organic carbon (TOC). ANC_{CB} is an alternative chemical criterion to describe the acid-base status and buffer capacity of water (Reuss and Johnson 1986), and it is defined as the equivalent sum of base cations minus the equivalent sum of strong mineral acid anions: $(Ca + Mg + Na + K) - (SO_4 + NO_3 + Cl)$. Non-marine xSO_4 and xBC were estimated as the differences between total concentrations and concentrations attributable to marine salts, the latter based on ratios to Cl^- in seawater.

Sampling of fish

Fish were sampled at a three-year interval with gill net series of eight 1.8×30 m nets of mesh sizes 12–60 mm in 1985–1992 (Raitaniemi *et al.*

1988). NORDIC multimesh survey nets (1.5×30 m; 12 panels with mesh sizes 5–55 mm, CEN 2005) have been used since 1995. For comparability, net panel area and selectivity corrections were calculated according to Tammi *et al.* (2004) and the catches from mesh sizes 5, 6.25, 8 and 10 mm of NORDIC nets were excluded from the analyses. The catch of each species was counted and total weight measured. Results concerning the fish status are expressed as NPUE (mean number of fish in one NORDIC survey net in one night). For length frequency distributions, the total length of all fishes was measured to the nearest cm and those sampled for age and growth to the nearest mm. The age of perch was determined from opercular bones and ascertained from otoliths for larger individuals. The age of roach was determined from scales and ascertained using cleithral bones for larger individuals. The growth was back-calculated using the Monastyrsky procedure for perch and Fraser-Lee for roach (Bagenal and Tesch 1978, Raitaniemi *et al.* 1988).

Statistical analyses

A non-parametric Mann-Kendall test (Z -statistics, *see* Hipel and McLeod 2005) was used for long-term trend analyses of changes in water quality and NPUE of perch and roach in the study lakes. No assumption of normality is required by the test and so the non-transformed original data were used in the analyses. For water quality parameters, the gradient of the trend (annual change), i.e. slope of the linear trend, was calculated according to Sen's slope estimation method (Sen 1968). Kruskal-Wallis or Mann-Whitney tests (SYSTAT 13) were used to examine significance of differences of perch and roach NPUE and growth between the periods before, during, and after the highest acidification impact.

Results

Water quality responses

The water chemistry records showed severe or moderate acidification in all study lakes in the late 1980s and early 1990s, which was indi-

cated by low alkalinity values commonly below $0 \mu\text{eq l}^{-1}$ (Tables 1 and 2, Fig. 1). However, improvement of water quality from severe acid conditions has taken place since the early 1990s. Sulphate concentrations have significantly

decreased and pH and buffering capacity have significantly increased from the late 1980s, showing clear signs of recovery from acidification for all 12 lakes (Tables 1 and 2). Base cation concentrations are still declining in the lakes,

Table 1. Mean alkalinity, pH, non-marine sulphate (xSO_4), total organic carbon (TOC) and labile aluminium (Al_{lab}) for the two comparative periods (1987 and 2005–2009 for alkalinity, pH, xSO_4 and TOC, 1987 and 2005 for Al_{lab}) in the 12 study lakes. The monitoring lakes are presented in groups representing four levels of fish population response to acidification. Group 1: perch extinct, group 2: perch affected, group 3: roach extinct, group 4: roach affected. n.d. = no chemical data.

Lake groups	Alkalinity ($\mu\text{eq l}^{-1}$)		pH		xSO_4 ($\mu\text{eq l}^{-1}$)		TOC (mg l^{-1})		Al_{lab} ($\mu\text{g l}^{-1}$)	
	1987	2005–2009	1987	2005–2009	1987	2005–2009	1987	2005–2009	1987	2005
Group 1										
Iso Lehmälampi	–36	–7	4.9	5.3	113	52	4.8	5.8	83	31
Iso Majaslampi	–33	–3	4.8	5.2	121	56	2.5	5.3	141	34
Hauklampi	–19	–4	4.9	5.4	161	75	2.8	3.9	276	64
Group 2										
Munajärvi	–15	–1	4.9	5.3	80	50	8.3	13.5	111	40
Orajärvi	–37	–3	4.9	5.5	134	53	1.5	3.8	161	< 10
Saaren Musta	–11	–3	5.2	5.1	145	71	2.3	8.0	66	54
Group 3										
Simijärvi	28	21	5.9	6.3	147	115	2.8	4.0	35	< 10
Isojärvi	53	45	5.6	6.0	157	97	5.0	7.1	28	< 10
Pitkäjärvi	1	28	5.2	6.1	130	81	3.9	6.2	40	11
Group 4										
Saarijärvi	n.d.									
Vitsjön	7	59	6.4	6.4	164	92	4.9	6.7	< 10	< 10
Kattilajärvi	10	30	6.0	6.2	165	99	3.6	5.6	19	< 10

Table 2. Trends of key chemical acidification variables during 1987–2009 in 12 integrated water chemistry and fish monitoring lakes of the present study. For the annual change ($\mu\text{eq l}^{-1} \text{yr}^{-1}$ for alkalinity, ANC_{CB} , H^+ , xSO_4 , xBC and $\text{NO}_3\text{-N}$; $\text{mg l}^{-1} \text{yr}^{-1}$ for TOC), statistically significant trends (Mann-Kendall test) are indicated with asterisks (***) $p < 0.001$, ** $p < 0.01$, * $p < 0.05$).

Lake groups	Trend data	Alkalinity ($\mu\text{eq l}^{-1} \text{yr}^{-1}$)	ANC_{CB}	H^+	xSO_4	xBC	$\text{NO}_3\text{-N}$	TOC ($\text{mg l}^{-1} \text{yr}^{-1}$)
Group 1								
Iso Lehmälampi	1987–2009	0.57*	0.94***	–0.38***	–3.24***	–2.32***	–0.03**	0.14**
Iso Majaslampi	1987–2007	1.76**	2.16*	–0.44*	–3.71**	–1.00	0.08	0.22
Hauklampi	1987–2007	1.44***	2.67***	–0.68***	–5.81***	–3.26***	–0.07*	0.13**
Group 2								
Munajärvi	1987–2006	1.20*	1.53	–0.73**	–2.75*	–0.88	–0.04	0.05
Orajärvi	1987–2006	1.20**	1.44	–0.62***	–5.00***	–3.32***	0.07*	0.11*
Saaren Musta	1987–2005	1.13**	1.68*	–0.23	–4.92***	–3.04***	–0.03	0.16*
Group 3								
Simijärvi	1987–2009	1.30***	0.18	–0.06**	–2.56***	–2.70***	–0.60***	0.06**
Isojärvi	1987–2006	2.00**	2.83***	–0.06***	–4.90***	–2.67***	–0.01	0.12**
Pitkäjärvi	1987–2006	2.00***	1.25**	–0.15***	–3.33***	–1.62***	–0.03	0.10*
Group 4								
Saarijärvi	n.d.							
Vitsjön	1987–2009	2.33***	1.64*	–0.02***	–4.97***	–3.49***	–0.02*	0.15***
Kattilajärvi	1987–2009	0.93**	0.40	–0.01*	–4.42***	–4.12***	–0.01*	0.10***

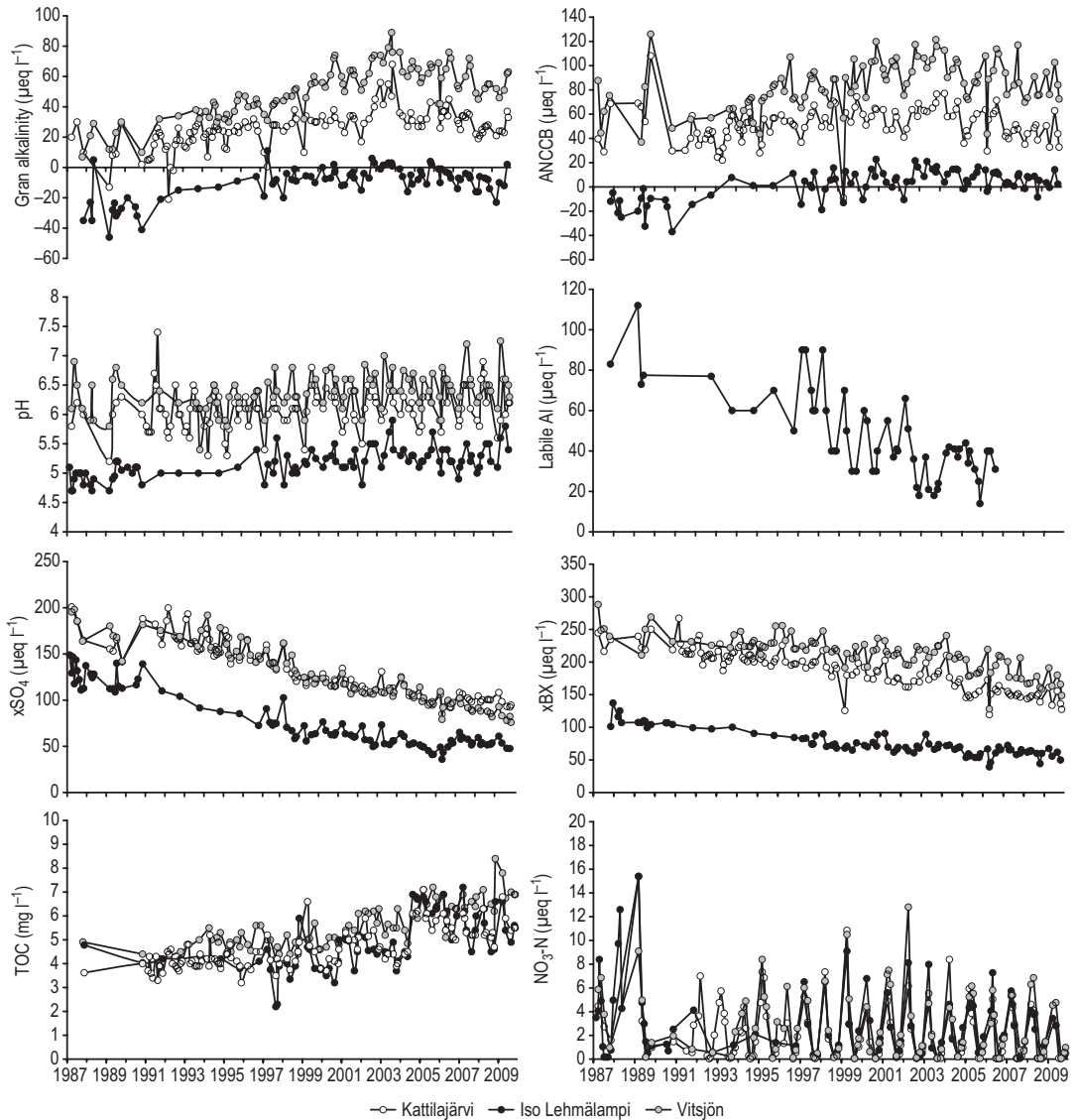


Fig. 1. Long-term trends of key chemical acidification parameters in three fish monitoring lakes in southern Finland (1987–2009).

but presumably to a lesser extent than sulphate. The less steep decline of lake water base cation concentrations as compared with that of sulphate (Fig. 1) resulted in improved acid–base status of soils and has led to increased buffering capacity of the lakes. Low pH is associated with high concentrations of labile aluminium, and a decrease in acidity is also reflected in decreasing labile aluminium concentrations in recovering lakes. The elevated labile aluminium concentrations ($\sim 80\text{--}300 \mu\text{g l}^{-1}$) in the late 1980s decreased in the

mid-2000s to a level of $< 10\text{--}60 \mu\text{g l}^{-1}$ (Table 1 and Fig. 1). Nitrate concentrations have also decreased in most of the study lakes. Contrary to minerogenic acidification, organic acidity — indicated by increasing TOC concentrations since the early 1990s and an elevated level since 2004 (Fig. 1) — has increased, resulting in a break of recovery of buffering capacity in the study lakes during the same period, evidenced by decreasing alkalinity (measured). At the same time charge-balance ANC (calculated) has also decreased.

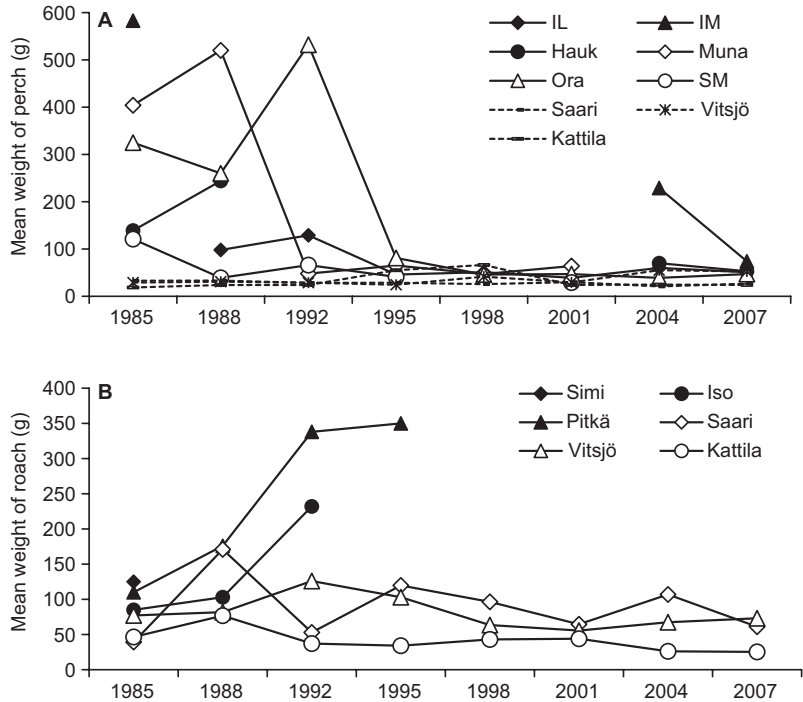


Fig. 2. Mean weight of (A) perch and (B) roach in lakes with lost populations (black symbols) and affected populations (white symbols). The mean weights of perch from three “roach-affected” lakes are given for comparison (dotted lines).

Responses of perch and roach populations

From the “perch-extinct” lakes of group 1, Iso Lehmälampi had lost its perch population before we started the monitoring in 1985. After re-introductions by local fishermen, a reproducing perch population has been present since 1988. We recorded the last original perch, large and old (≥ 7 years) individuals, in Iso Majaslampi in 1985 and in Hauklampi in 1988 (Fig. 2), but after that the populations were extinct as no perch were caught in the test fishings in later years. After a successful re-introduction in 2002, both lakes are now inhabited by reproducing populations (Nyberg *et al* 2010). The last roach from “roach-extinct” lakes of group 3, also large and old (12–15 years) individuals, were captured in 1985, 1992 and 1995 in lakes Simijärvi, Isojärvi and Pitkälampi, respectively (Fig. 2), but no roach were observed after that in any of these lakes.

New strong year-classes of perch appeared in the populations of “perch-affected” lakes of group 2 in the mid-1990s indicating recovery of perch reproduction. Perch NPUE increased correspondingly (Fig. 3) and the trend was significant (Table 3). At the same time, no clear

response or significant trend could be seen in the roach populations of “roach-affected” lakes of group 4 (Fig. 3 and Table 3). A comparison of pooled values of NPUE in the years of high acidification pressure with those in the years of recovery showed a statistically significant difference for perch (Mann-Whitney U -test: $U = 0$, $p < 0.001$) but not for roach (Mann-Whitney U -test: $U = 77.5$, $p > 0.1$).

The recovery of perch reproduction in Oranjärvi caused a drastic change in the population structure. Besides an almost tenfold increase in NPUE, from 1995 onwards the test-fishing catches consisted almost entirely of small perch, the mean weight being < 50 g (Fig. 2) and the length 10–15 cm (Fig. 4). The strongest year-class after the onset of recovery was born in 1992, and since then successful reproduction of perch took place each year (Fig. 5). The growth of perch in Oranjärvi was fairly slow in year-classes born in the 1960s (Fig. 5). The length of 20 cm was exceeded at the age of 8–10 years. In the year-classes of the 1970s, the growth had accelerated and the fastest growth was recorded in the year-classes of the late 1980s. Perch of the year-class 1988 reached the total length of close to 30 cm in four years (Fig. 5). After the appearance of strong

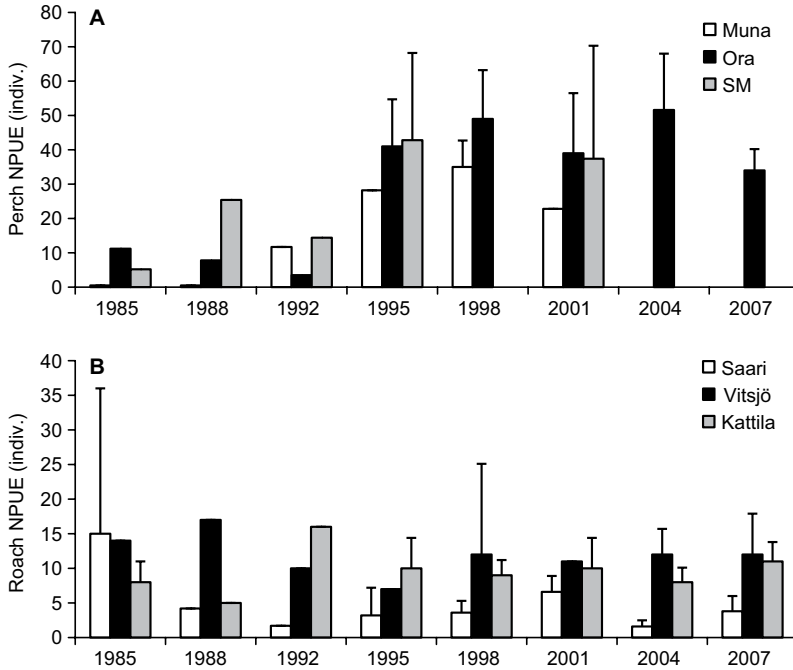


Fig. 3. The number (NPUE, mean + SD in the years of > 1 test-fishing efforts) of (A) perch and (B) roach in the gillnet catches of lakes with affected populations. (SM = Saaren Musta).

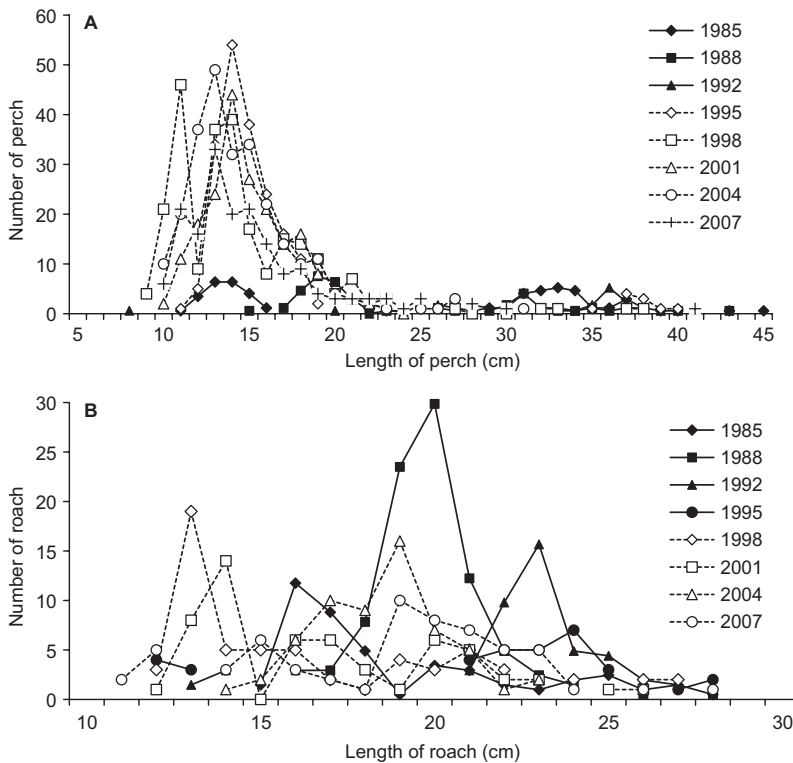


Fig. 4. Length frequency distribution of (A) perch in Oräjärvi and (B) roach in Vitsjön during 1985–2007. Black symbols refer to the years of highest acidification impact on the populations, open symbols to the years of recovery.

year-classes from the early 1990s and onwards, a drastic decrease in growth took place, to a rate typical of dense perch populations and rather sim-

ilar to that recorded in fish from the year-classes of the 1960s. The growth was significantly faster during the 1970s and the 1980s, the decades of

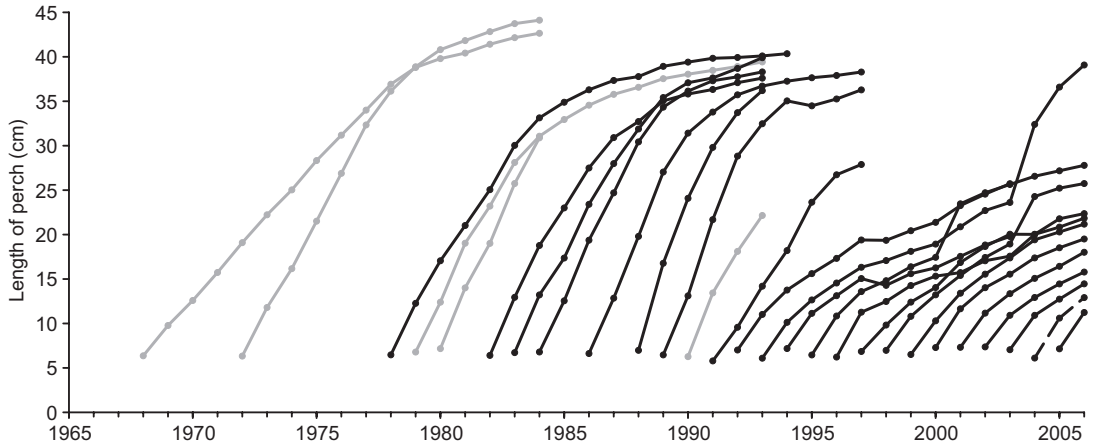


Fig. 5. Back-calculated growth of the year-classes 1968–2005 for perch in Orajärvi ($n = 633$). The growth curves based on 2–5 individuals are grey.

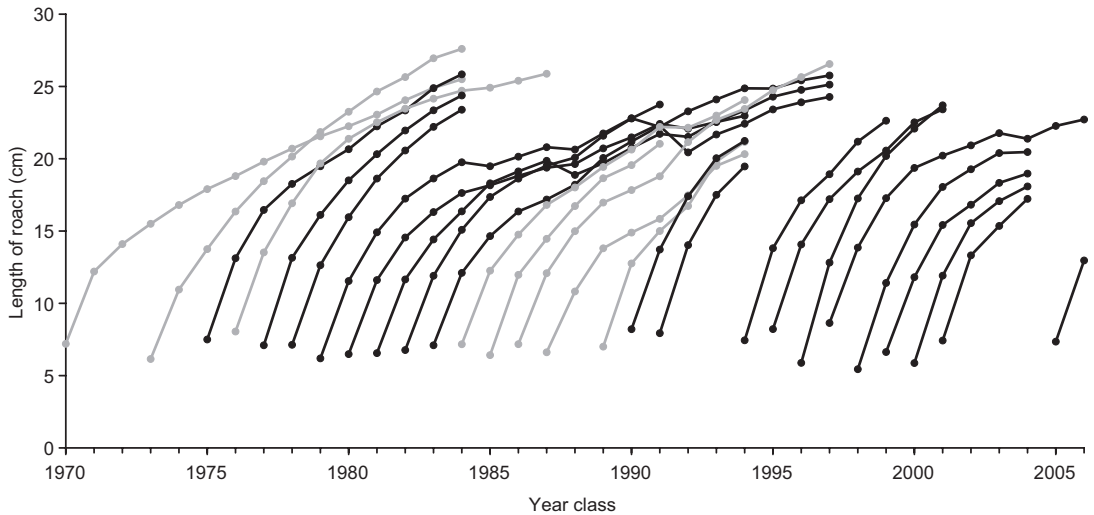


Fig. 6. Back-calculated growth of the year-classes 1970–2005 for roach in Vitsjön ($n = 346$). The growth curves based on 2–5 individuals are grey.

the highest acidification impact, as compared with that in the years before (the 1960s) and the time of recovery since the 1990s (Kruskal-Wallis test statistic for 5-year-old fish 19.7, $p < 0.001$). The pairwise comparison indicated no significant difference between the growth rate of year-classes of the 1960s and the 1990s (Conover-Inman test statistic 0.24, $p > 0.1$).

In most years of the first decade of the study, the roach population in Vitsjön was dominated by fish > 20 cm total length (Fig. 4), most of them born in 1978–1983 (Fig. 6). The low number of

small roach in that time was interpreted to be due to acidification-induced failures in reproduction during a ten year period from mid 1980s to mid 1990s. Smaller roach of < 15 cm from year-classes 1997–1999 appeared in the catches in 1998 and 2001, suggesting some recovery in reproduction (Fig. 4). However, no strong year-classes of roach were recorded in the lake during the 2000s. The fish born in the early 1970s and those born around the year 1980 exceeded the total length of 20 cm at the age of 8–9 years. Roach from year-classes born in the mid-1970s

and those born in the mid-1990s grew somewhat faster and exceeded the length of 20 cm at the age of 4–5 years (Fig. 6). Thus, growth variation between year-classes was considerable, and there were no statistically significant differences when the growth of year-classes born before, during and after the highest acidification impact (see Fig. 6) were compared (Kruskal-Wallis test statistic for 5 year old fish 2.1, $p > 0.1$).

Discussion

Water quality

The present study provides good evidence that emission reduction measures led to regional-scale recovery from acidification in sensitive ecosystems in Finland. Along with sulphate, there is in general a decrease in nitrate concentrations in acid-sensitive Finnish forest lakes although $\text{NO}_3\text{-N}$ plays only a minor role in the acidity status and as an acidifying agent in Finnish lakes (Mannio 2001a, 2001b, Vuorenmaa and Forsius 2008). Nitrate concentrations in Finnish lakes are in general very low, and acidity is predominantly regulated by organic anions and sulphate (Kortelainen *et al.* 1989).

In conditions of decreasing minerogenic acidification, increased catchment-derived organic acidity has become proportionally more important in affecting recovery process of sensitive lakes in Finland (Vuorenmaa 2007). Increasing TOC concentrations throughout the 1990s and the 2000s, as observed in Norway, Sweden, UK and North America can also be recorded in small forest lakes in Finland (Vuorenmaa *et al.* 2006, Monteith *et al.* 2007) and also in the present study. Monteith *et al.* (2007) suggested that the increase in TOC concentration is related to the recovery from acidification, i.e. decreasing sulphate deposition and improved acid-base status of the soil. Elevated TOC concentrations in the study lakes were observed particularly in the late 2000s, due to rainy summers and autumns in 2004 and 2006 (Nyberg *et al.* 2010). Leaching of humic matter from the catchment, inducing higher organic acidity in the lakes, can be an important factor suppressing recovery of pH and alkalinity in sensitive Finnish lakes (Wright *et al.*

2006, Vuorenmaa 2007, Vuorenmaa and Forsius 2008).

Sarkkola *et al.* (2009) studied trends in stream water TOC concentrations in eight, forested headwater catchments in eastern Finland. The mean annual TOC concentration increased significantly in seven of the eight catchments. According to mixed model regression analysis, stream water temperature, precipitation and peatland percentage of the catchment were the most important variables explaining annual and most seasonal TOC concentrations. Although the atmospheric deposition of SO_4 , NH_4 , and NO_3 decreased significantly over the study period, no significant link with TOC concentration was found. In contrast, stream water TOC concentrations were mainly driven by catchment characteristics and hydrometeorological factors rather than trends in atmospheric acid deposition.

Climate change may increase the mobilization and export of DOC and organic acidity to surface waters, which in turn may delay recovery from acidification (e.g. Evans *et al.* 2005, Holmberg *et al.* 2006, Wright *et al.* 2006, Posch *et al.* 2008). The potential impact of mobilization and export of DOC and organic acidity may become particularly important in Finnish conditions because of the large stores of organic matter in boreal forest soils (Vuorenmaa and Forsius 2008) and peatlands (Sarkkola *et al.* 2009).

Fish

Perch, as an acid-tolerant species, was responding rapidly to improved water quality, and the first signs of population recoveries were detected in the early 1990s (Nyberg *et al.* 1995, Rask *et al.* 1995b). According to the observations and trends of the present study, the structure of affected perch populations has returned to normal during the monitoring period. Successful re-establishment of disappeared perch populations into previously heavily acidified lakes (lake group 1) further emphasizes the importance of the chemical recovery of the lakes (Nyberg *et al.* 2010).

Our growth data for perch from Orajärvi, including samples from the year-classes 1964–2006, a period of more than 40 years, illustrates the entire history of acid rain impacts on the fish

population of a single lake. Although we had the data only from a few perch born in the 1960s, their slow growth suggests that the population density in those years was high or normal with no impacts of acidification on reproduction. This is also supported by paleolimnological records, suggesting that a rapid acidification of the lake started in the 1960s (Tolonen and Jaakkola 1983). The striking increase of growth towards the late 1980s is an excellent indication of flexibility of the perch in changing circumstances, in this case to declining population density due to acidity-induced reproduction failures in the 1970s and the 1980s. It is worth attention that the fast growth rate was possible with invertebrate diet, for example *Asellus aquaticus*, as no fish food was available (Raitaniemi *et al.* 1988). The sharp decrease of growth after the onset of recovery and new strong year-classes further emphasizes the density dependent growth pattern of perch.

For more acid-sensitive species like roach, little if any recovery of affected populations was recorded. Neither the abundance nor the growth of roach showed significant responses to the chemical recovery of the study lakes. This may indicate that water chemistry is still critical for the success of roach populations, and evidently more time and more suitable water quality are needed for a distinct recovery. The appearance of some stronger year-classes of roach in Vitsjön in the late 1990s, following the weak or missing ones between mid 1980s and mid 1990s, looked like an onset of recovery, but the year-classes of the 2000s remained scarce again. As compared with results of other studies from small Finnish lakes (Raitaniemi and Rask 1990, Rask and Tuunainen 1990, Estlander *et al.* 2010), the growth of roach in Vitsjön was faster throughout the study period, suggesting that intraspecific or interspecific food competition was lower.

Perch is a generalist carnivore feeder, during its life span usually shifting from zooplankton to zoobenthos and further to fish (Allen 1935, Persson 1994, Horppila *et al.* 2000). Roach is an omnivore feeding on zooplankton and zoobenthos and later turning to detritus and macrophytes (Horppila *et al.* 2000, Estlander *et al.* 2010). Thus, these species have a competitive interaction when feeding on zooplankton in their first years. As perch is a visual feeder,

light conditions are of importance, and clear water is favouring perch (Estlander *et al.* 2012). Moreover, large perch can prey on roach, which may delay the recovery of a roach population in conditions of critical water quality like in the case of Vitsjön. In poor light conditions, decreased feeding efficiency of perch has been shown (Bergman 1988, Estlander *et al.* 2012), as well as dominance of roach over perch in competition for zooplankton food in turbid waters of eutrophicated lakes (Persson 1983, Olin *et al.* 2002) or in highly humic lakes (Estlander *et al.* 2010, Olin *et al.* 2010). Consequently, the recent increasing trends in TOC and water colour of lakes, could favour roach if acidity — either minerogenic or organic — did not disturb the reproduction of roach.

To conclude, the chemical recovery of the study lakes was clearly followed by biological recovery, especially of perch populations. Thus, the present findings indicate success in the ultimate intention of the emission abatement policy. The findings of the present study also emphasize the importance and value of integrated monitoring approach including both physical, chemical and biological variables, and the suitability of small headwater lakes for such monitoring.

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