BOREAL ENVIRONMENT RESEARCH 15: 480–490
ISSN 1239-6095 (print) ISSN 1797-2469 (online)

Helsinki 29 October 2010

Re-establishment of perch in three lakes recovering from acidification: rapid growth associated with abundant food resources

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Received 18 Mar. 2009, accepted 14 Oct. 2009 (Editor in charge of this article: Outi Heikinheimo)

Nyberg, K., Vuorenmaa, J., Tammi, J., Nummi, P., Väänänen, V.-M., Mannio, J. & Rask, M. 2010: Re-establishment of perch in three lakes recovering from acidification: rapid growth associated with abundant food resources. *Boreal Env. Res.* 15: 480–490.

In 2002, we reintroduced perch (*Perca fluviatilis*) into three small, previously heavily acidified and fishless lakes. Test fishing indicated that released perch had survived in all three study lakes and reproduced successfully in two of them. Growth of introduced individuals had increased sharply after introduction. The increased growth of perch was an apparent consequence of high abundance of macroinvertebrates in the fishless lakes. Activity traps indicated even a 90% decrease in the numbers and size of invertebrates upon the fish releases: a very likely response to the predation by the stocked perch. Our observations indicate that the chemical recovery of the study lakes from acidification has been remarkable enough to allow recolonization by aquatic organisms. For perch, and probably for other acid tolerant fish, this means the possibility of a successful re-establishment of populations in previously acidified fishless lakes which, in turn, increases the value of such lakes for fishing.

Introduction

Sulphate deposition has been the major driving force in the anthropogenic acidification of surface waters in the Nordic Countries (Finland, Sweden, Norway) (Skjelkvåle *et al.* 2001) and elsewhere in Europe (Prechtel *et al.* 2001, Wright *et al.* 2005), and has resulted in lost and damaged fish stocks and reduced biodiversity. In the lakes of Norway, Sweden and Finland, altogether ca. 10 000 fish populations were assessed to be lost due to acidification (Tammi *et al.* 2003). In Finland, it was estimated that 990–2050 fish populations, mainly roach (*Rutilus rutilus*), died out in acidified lakes (Rask *et al.* 1995). After the disappearance of fish, macroinvertebrate predators became important in controlling the structure and function of aquatic food chains (Eriksson *et al.* 1980, Appelberg *et al.* 1993, Rask *et al.* 2001). According to the fish status surveys cited above, perch was not extinct in any Finnish lakes larger than 0.04 km^2 (Tammi *et al*. 2003) or > 0.01 km^2 (Rask *et al*. 1995) but from our monitoring data and sources of local information we know cases of complete disappearance of perch due to acidification (Rask and Tuunainen 1990, Rask *et al*. 1995). Further, as there are ca. 130 000 lakes < 0.01 km^2 in Finland (Raatikainen and Kuusisto 1985), it can be presumed that the total number of lost perch populations may be some hundreds.

Following the general decreasing trends in sulphur emissions (Lövblad *et al*. 2004) and deposition (e.g. Barrett *et al*. 2000, Prechtel *et al*. 2001), chemical recovery from acidification of sensitive surface waters, indicated by decreasing concentrations of sulphate and a subsequent increase in pH and buffering capacity (alkalinity), was observed during the 1990s in Finland (Mannio 2001, Forsius *et al*. 2003, Tammi *et al*. 2004, Vuorenmaa and Forsius 2008) and in many parts of Europe and North America (Stoddard *et al*. 1999, Evans *et al*. 2001, Skjelkvåle *et al*. 2005). As a result of improved water quality in acidified Finnish lakes, signs of a process of biological recovery in perch (*Perca fluviatilis*) populations have been recorded since the early 1990s in lakes that had experienced severe acid-induced fish population reductions during the 1970s and 1980s (Nyberg *et al*. 1995, 2001, Tammi *et al*. 2004).

After these observations we started an experiment to restore the perch populations by introducing fish into three acidified and fishless lakes. Three aims set for the study were as follows: (1) to see whether the water chemistry has recovered toward the suitable level for the newly introduced perch to survive in the experimental lakes, (2) whether they succeed in reproduction, and if so, (3) what kind of responses could be seen in the invertebrate fauna of the lakes. Re-establishment of fish population, can be seen as a management method for restoration of previously acidified fishless lakes. Perch can also be seen as an indicator species for re-establishment of the stocks of other relatively acid-tolerant fish species, for example pike (*Esox lucius*) (Rask and Tuunainen 1990). Successful re-establishment of fish populations may increase the value of such lakes for recreational fishing.

Material and methods

Study lakes

The study comprised three forest lakes (Iso Majaslampi, Pieni Majaslampi and Hauklampi) located in Nuuksio upland region in the southern Finland about 30 km NW from Helsinki. The Nuuksio area has been exposed to high air-pollution load of acidifying compounds from local emission sources, as well as transported from large emissions areas in central-eastern Europe. As many other upland lakes in the area, the study lakes are susceptible to acidifying deposition due to the acid-sensitive geological characteristics of the local soil and bedrock in the catchments (Pätilä 1986). The severe acidification in the most sensitive lakes in the Nuuksio area started in the early 1960s (Tolonen and Jaakkola 1983). The study lakes are small (0.011–0.063 km^2), closed seepage or headwater lakes with low catchment-to-lake ratio (< 10). Their catchments are covered mainly by coniferous forests and range from 0.04 to 0.33 km^2, of which 40%–48% is exposed bedrock with soil thickness less than 1 m, and 2%–23% peatland (Peura 1990; Finnish Environment Institute, the information system of Finland's surface waters). Chemically, the lakes can be characterized as acid-sensitive clear-water oligotrophic lakes (total phosphorus usually < 10 $\mu g\ l^{-1}$ during the dormant season) with low content of humic material (total organic carbon (TOC) usually < 5 mg l^{-1}), low base cation concentration, low alkalinity, low pH and elevated labile aluminium concentrations (Table 1).

Water chemistry sampling

Samples for water chemistry analyses were taken either from the middle of the lake (1 m depth) or at the outlet, during the autumn thermal overturn phase. Hauklampi was sampled in 1984, 1986, and 1987 and annually during 1989–2007. Iso Majaslampi and Pieni Majaslampi were sampled in 1984, 1986, 1987 and 1989, and annually during 2000–2007. The chemical analyses covering 25 variables were carried out by the laboratory of the Finnish Environment Institute according to the standardized methods (Forsius *et al*. 1990, Vuorenmaa 2007). In this study, the main emphasis is placed on parameters reflecting changes in acidification status and chemical recovery: alkalinity (Gran method) and pH, charge-balance ANC (ANC_{CB}) non-marine sulphate (x_{SO4}), non-marine base cations $x_{BC} = (x_{Ca} + x_{Mg} + x_{Na} + x_K)$ and TOC. Calculated acid neutralizing capacity (charge balance ANC_{CB}) was defined as the equivalent sum of base cations minus the equivalent sum of strong acid anions (Ca + Mg + Na + K) – (SO_4 + NO_3 + Cl). For labile aluminium (Al_{lab}), total reactive and non-labile fractions of aluminium were determined by spectrophotometric determination with pyrocatechoviolet (FIA analyzer). Labile aluminium was calculated by subtracting non-labile aluminium from the total reactive aluminium. Measurements of aluminum fractions (Al_{lab}) were available for the years 1987 and 1992–2005. The development of ANC_{CB} is not affected by TOC changes (organic acidity), reflecting more directly changes in SO_4 and minerogenic acidity. ANC_{CB} has been therefore proposed as an integrating single criterion in assessing biological damage by acidification (e.g. Henriksen *et al*. 1992). x_{SO4} and x_{BC} are calculated as non-marine fractions estimated as the differences between total concentrations and concentrations attributable to marine salts, the latter based on ratios to Cl in seawater.

Perch stocking and sampling

Perch were reintroduced to Hauklampi, Iso Majaslampi and Pieni Majaslampi in 2002. The lakes had lost their perch populations by the end of 1980s (Raitaniemi *et al*. 1988, Rask *et al*. 1995), and our test fishing with gillnets in autumn 2001 proved that they were still fishless. The perch to be introduced to the lakes were caught from Iso-Valkjärvi, a small acidic forest lake situated ca. 150 km north of the Nuuksio upland region. The perch in Iso-Valkjärvi are adapted to acidic conditions, pH levels 5.0–5.5 (Rask and Virtanen 1986, Järvinen *et al*. 1995), and thus they were thought to be most suitable for our experiment. Perch were caught in spring (May) and in autumn (September) with iron-wired trap nets (mesh size 10 mm) to ascertain the inclusion of both sexes, because according to our observations trap catches consist mainly of males in spring and of females in autumn. Altogether 534 perch were stocked in the three lakes, of which 388 were fin clipped (left pelvic fin) and stocked in May, and 146 also fin clipped (right pelvic fin) stocked in September (mean length = 12.6 cm, SD = 1.2 cm, range = 9.0–17.0 cm). The fin clippings were carried out to distinguish between the stocked perch and their possible unmarked offspring. The total number of stocked perch in Hauklampi was 187, in

Table 1. Catchment characteristics and median values (2002–2007) for pH, Gran alkalinity, acid neutralizing capacity ANC ([Ca + Mg + Na + K] – [SO_4 + NO_3 + Cl]), labile aluminum (Al_{lab}), sum of non-marine base cations (x_{BC}), non-marine sulphate (x_{SO4}) and calcium (x_{Ca}), total organic carbon (TOC) and total phosphorus (P_{tot}) in the study lakes. The ranges (min-max) for chemical variables are presented in parenthesis.

	Hauklampi	Iso Majaslampi	Pieni Majaslampi
Area (km^{-2})	0.025	0.063	0.011
Catchment area (km^{-2})	0.21	0.33	0.04
Depth (m)	4.7	8.9	6.5
Exposed bedrock (%)	48	40	46
Peatland (%)	13	2	23
pH	5.5 (5.1 to 5.9)	5.1 (4.9 to 5.5)	5.2 (5.0 to 5.3)
Gran alkalinity (μeq l^{-1})	–2 (–14 to 11)	–9 (–19 to 5)	–9 (–14 to –5)
ANC (μeq l^{-1})	2 (–5 to 22)	–3 (–12 to 6)	–6 (–7 to –1)
Al lab (μg l^{-1})	54 (14 to 110)	64 (34 to 89)	61 (29 to 88)
x_{BC} (μeq l^{-1})	79 (70 to 107)	63 (46 to 64)	53 (41 to 55)
x_{Ca} (μeq l^{-1})	33 (29 to 53)	36 (29 to 39)	28 (24 to 34)
x_{SO4} (μeq l^{-1})	78 (69 to 83)	60 (49 to 75)	55 (47 to 61)
TOC (mg l^{-1})	4.0 (3.1 to 5.2)	4.8 (2.3 to 6.3)	3.2 (1.5 to 4.4)
P_{tot} (μg l^{-1})	4 (2 to 5)	5 (3 to 6)	4 (3 to 7)

Iso Majaslampi 215, and in Pieni Majaslampi 132 (Table 2).

Test fishings were carried out using NORDIC multimesh gillnets (Appelberg *et al*. 1995, European Standard EN 14757:2005) in August 2004 and 2007. Benthic gillnets (total length 30 m, height 1.5 m, panel length 2.5 m with mesh sizes 43, 19.5, 6.25, 10, 55, 8, 12.5, 24, 15.5, 5, 35 and 29 mm) were set before the sunset (3 nets to Hauklampi and Pieni Majaslampi, 5 nets to Iso Majaslampi) and kept in the lakes until the next morning, i.e. for ca. 12 h. Total length and weight of every perch were measured, their sex determined, fin clipping identified and stomach contents examined to detect possible cannibalism. The age of perch was determined from burned and crosswise split otoliths (Appelberg *et al*. 1995). Back calculation of length growth was made from opercular bones using Monastyrsky's procedure (Bagenal and Tesch 1978) ($b = 0.88$; Raitaniemi *et al*. 1988).

Invertebrate sampling

Nektonic and benthic invertebrates were sampled during 2002–2007 with activity traps which give an index of abundance. Invertebrate trappings were carried out between 13 May and 15 June, except in 2003 when invertebrates were trapped during 17–19 September. Glass jars (volume 1 litre) equipped with a funnel (diameter 100 mm in the large and 23 mm in the narrow end) were used as traps (Elmberg *et al*. 1992). In each of the lakes, 10 traps were used each year. The traps were placed horizontally on the bottom by the shore at depths of 0.25–0.75 m, and left for 48 h. The traps were ca. 3-m apart parallel to the shoreline. In each lake, we used the same trapping place every year. On emptying, trap contents were passed through a 1 mm-sieve, and the remaining animals were counted and classified.

Invertebrates in the traps were grouped following the taxon list by Nudds and Bowlby (1984). Furthermore, animals were assigned to five size classes (0–2.5 mm, 2.6–7.5 mm, 7.6–12.5 mm, 12.6–20.0 mm and ≥ 20.1 mm) according to Nudds and Bowlby (1984), with small modifications (*see* Elmberg *et al*. 1992). Invertebrate biomass was indexed by using the average catch per trap multiplied by the number of each prey taxon according to its average size.

Results

Water chemistry

The water chemistry records showed severe acidification of the study lakes during the 1980s and early 1990s, indicated by low pH (< 5) and elevated labile aluminium concentrations (in Hauklampi > 250 μg l^{-1}). Moreover, buffering capac-

Table 2. The number, density, length range and weight-range of perch stocked into the experimental lakes in 2002, and number, length range and weight-range of stocked perch in gillnet catches in the test fishings in 2004 and 2007.

Lake	Stocked perch (total, ind.)	Stocked perch (ind. ha^{-1})	Catch of stocked perch (ind.)	Catch of stocked perch (%)	Length range (cm)	Weigth range (g)
Hauklampi						
2002	187	75			10–16	10–50
2004			22	11.8	22–26	118–217
2007			6	3.2	23–25	112–167
Iso Majaslampi						
2002	215	34			10–17	10–56
2004			17	7.9	23–31	144–374
2007			2	0.9	30–31	323–407
Pieni Majaslampi						
2002	132	120			9–17	9–56
2004			18	13.6	18–28	151–289
2007			1	0.7	30	393

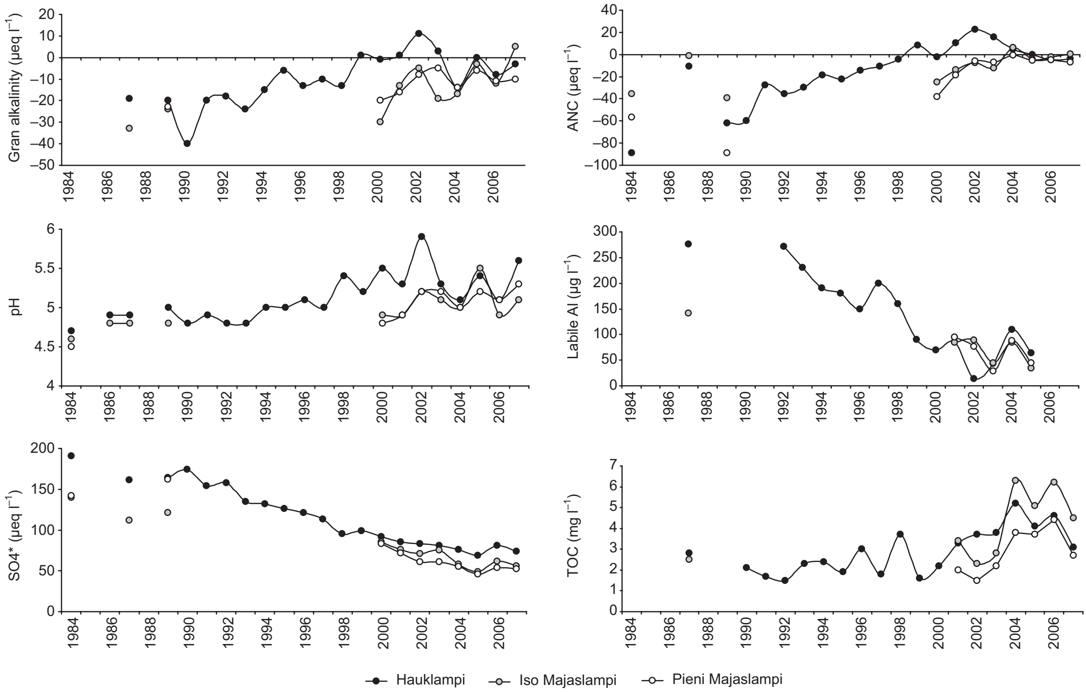

Fig. 1. Gran-alkanity, acid neutralizing capacity (ANC), pH, labile Al, sulphate and total organic carbon (TOC) values of Hauklampi, Iso Majaslampi and Pieni Majaslampi water samples 1984–2007.

ity in these lakes was poor during the 1980s and 1990s, with alkalinity (measured) and charge-balance ANC_{CB} (calculated) values commonly < 0 μeq l^{-1} (Fig. 1). However, improvement of water quality from chronic acid conditions has taken place in all study lakes. Sulphate concentrations have decreased and pH and buffering capacity have increased since the late 1980s to date. The elevated labile-aluminium concentrations in Hauklampi in the early 1990s decreased in the early 2000s to the level of 20–100 μg l^{-1}. Contrary to minerogenic acidification, organic acidity, indicated by elevated TOC concentrations, increased during the 2000s (Fig. 1).

The abundance, growth and diet of perch

Test fishing in August 2004 and 2007 indicated that the perch had survived in all the study lakes (Table 2) and reproduced in two of them (Table 3). The total catch of perch in 2004 was 3924–4472 g and 18–52 individuals in the three lakes (Table 3). In 2007, the corresponding values were 393–3228 g and 1–45 individuals. Catch per unit of effort (CPUE) values were 131–1328 g and 1–17 individuals per gillnet night during the study period. Perch born in their present lakes were captured from Hauklampi (n = 69) and Iso Majaslampi (n = 46) whereas no lake-born perch were caught from Pieni Majaslampi (Table 3).

The length ranges of the perch caught from Hauklampi, Iso Majaslampi and Pieni Majaslampi was 11–26 cm, 6–31 cm and 18–30 cm, respectively (Fig. 2). The age determination of perch sampled from Hauklampi and Iso Majaslampi revealed that all perch smaller than 20 cm had been born in 2003 or later. In addition, three larger perch caught from Iso Majaslampi in 2007 were born in the lake in 2003. In Hauklampi, perch born in 2003 constituted the strongest year-class born in the lake with a total of 66 individuals in the test fishing catches of 2004 and 2007, whereas only three perch born in 2006 were caught. In Iso Majaslampi, the strongest year-class so far was born in 2006 (n = 38). In addition, three perch born in 2005 and two born in 2007 were caught.

A sudden increase in growth of perch appeared after stocking in all three lakes (Fig. 3).

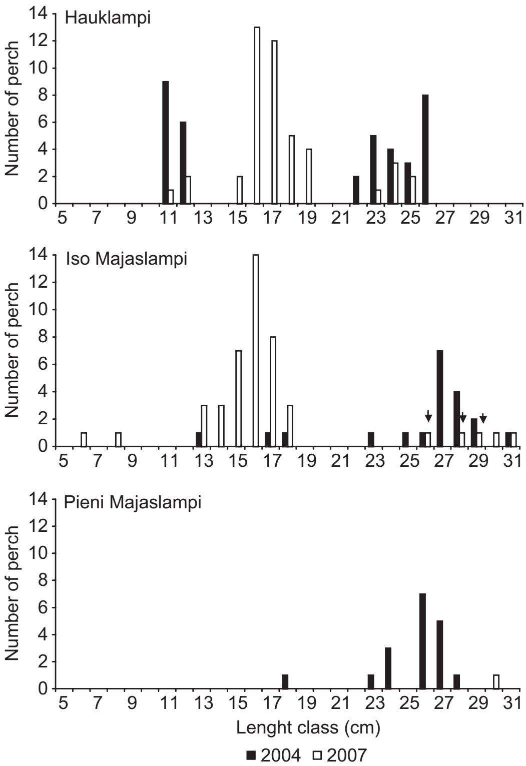

Fig. 2. Length distribution of the perch caught from Hauklampi (2004; n = 52, 2007; n = 45), Iso Majaslampi (n = 20 and 45 in 2004 and 2007, respectively) and Pieni Majaslampi (n = 18 and 1 in 2004 and 2007, respectively). Perch smaller than 20 cm in Hauklampi and in Iso Majaslampi were born in the lake and so were three larger individuals in Iso Majaslampi (indicated with arrows).

Three- to eight-year-old fish of 12–14 cm mean length at stocking had grown to mean lengths of 24–26.8 cm at the time of the test fishing in the late summer of 2004. According to the total length of the captured fishes, differences in growth were statistically significant in the order Iso Majaslampi > Pieni Majaslampi > Hauklampi (ANOVA: $F_{2,56} = 19.094$, $p < 0.001$; pairwise Tukey Iso Majaslampi *vs*. Pieni Majaslampi $p = 0.027$, Iso Majaslampi *vs*. Hauklampi $p < 0.001$ and Pieni Majaslampi *vs*. Hauklampi $p = 0.006$). No significant growth differences were recorded between the male and female perch (Iso Majaslampi $t_{15} = 2.02$, $p = 0.068$; Pieni Majaslampi $t_{16} = –0.617$, $p = 0.546$; Hauklampi $t_{20} = –0.437$, $p = 0.688$).

The most rapid growth of perch in all three lakes took place during the first summer after stocking and resulted in an average annual length increment of 6.6–7.0 cm for perch of the most abundant year class of stocked perch, born in 1994, with no significant differences between the lakes (Fig. 4; ANOVA: $F_{2,39} = 0.633$, $p = 0.536$). In the second summer, the growth of perch in Iso Majaslampi remained significantly faster with the average length increment of 5.1 cm as compared with that in Hauklampi and Pieni Majaslampi with the average length increments of 3.6 and 3.9 cm, respectively (Fig. 4; ANOVA: $F_{2,39} = 10.604$, $p < 0.001$; Tukey Iso Majaslampi *vs*. Hauklampi $p < 0.001$ and Iso Majaslampi *vs*. Pieni Majaslampi $p < 0.009$).

The lake-born perch appeared to grow faster in Iso Majaslampi than in Hauklampi. The perch of the year-class 2003 in Iso Majaslampi, 4+-year-old in summer 2007, had a mean total length of 27.1 cm (range = 25.5–28.4 cm, n = 3), whereas the fish of same age in Hauklampi showed corresponding values of 16.4 cm (range = 14.9–18.6 cm, n = 36; Fig. 3). Although

Table 3. Total catches and catch per unit of effort (CPUE) of test fishing in 2004 and 2007, and the number of lake born perch in the catches.

Lake	Total catch of perch (ind.)	Total catch of perch (g)	CPUE (ind. net^{-1})	CPUE (g net^{-1})	Lake-born perch (ind.)
Hauklampi					
2004	52	3985	17	1328	30
2007	45	2404	15	801	39
Iso Majaslampi					
2004	20	4472	4	894	3
2007	45	3228	9	646	43
Pieni Majaslampi					
2004	18	3924	6	1308	0
2007	1	393	< 1	131	0

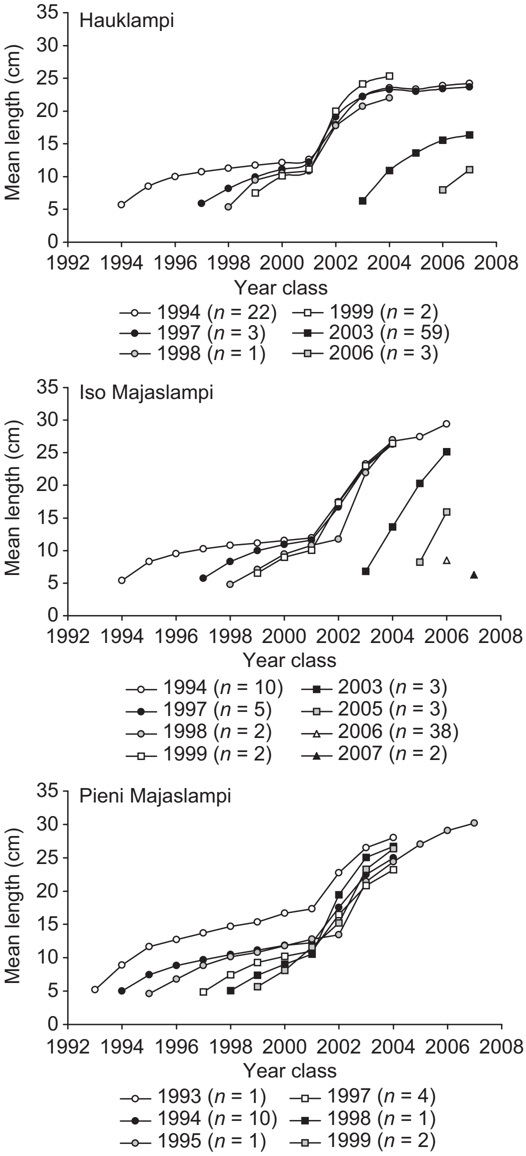

Fig. 3. Back calculated mean length growth of perch in Hauklampi, Iso Majaslampi and Pieni Majaslampi. Combined data of years 2004 and 2007. Perch were reintroduced in the study lakes in 2002. So, every perch year class after 2002 was born in Hauklampi and Iso Majaslampi. Numbers in parentheses show the count of perch in every year class.

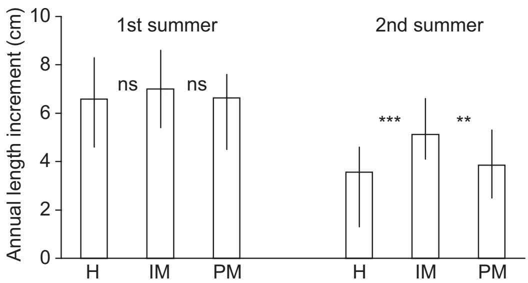

Fig. 4. The first and second summer length increments (mean ± range) of stocked perch of the year-class 1994 in studied lakes. H = Hauklampi (n = 22), IM = Iso Majaslampi (n = 10), PM = Pieni Majaslampi (n = 10).

the perch year-class 2006 appeared to be more abundant in Iso Majaslampi (n = 38 in test fishing catch 2007) than in Hauklampi (n = 3), the perch in Iso Majaslampi grew faster with the mean length of 15.3 cm (range = 12.4–17.2 cm) as compared with that in Hauklampi (mean length = 11.1 cm, range = 10.6–11.4 cm; Fig. 3). Yet, the growth of the age group 1+ perch of the "strong" year class 2006 in Iso Majaslampi was faster as compared with the 1+ fish of the "strong" year class 2003 in Hauklampi (t_{51} = 17.447, $p < 0.001$). Although natural year-to-year variations in the growth of perch are taken into account, the 4.2 cm difference in the mean length of 1+ perch of Iso Majaslampi in 2007 as compared with 1+ perch of Hauklampi in 2004 supports our view of faster growth of lake-born perch in the former lake.

The diet of stocked perch was almost completely dominated by macroinvertebrates. Stomach content examination indicated only three cases in Hauklampi where the stocked perch had eaten perch of the age group 1+ in summer 2004. No remains of 0+ perch were detected in the stomachs of stocked perch from any of the lakes.

Invertebrate abundance

Both the number and biomass indices of invertebrates collapsed in all three lakes after reintroduction the perch (Fig. 5). In Hauklampi and Iso Majaslampi where the perch were breeding successfully (Fig. 2), also the numbers and biomasses of invertebrates remained at the low level over the study period. As compared with the other lakes, in Pieni Majaslampi the number and biomass of invertebrates showed more variation, but the values were clearly smaller than those recorded prior to perch restocking (Fig. 5). In the activity trap catches, Dytiscidae were most

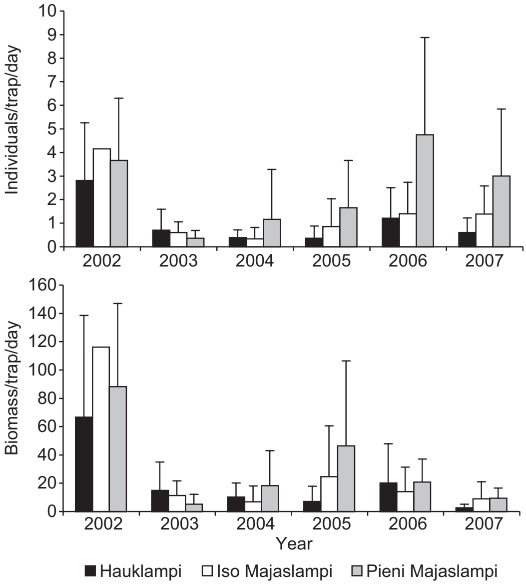

Fig. 5. Mean numbers (individuals/trap/day) (top) and biomass indices (biomass/trap/day) (bottom) of invertebrates (+ SD) in Hauklampi, Iso Majaslampi and Pieni Majaslampi during 2002–2007 as revealed by activity trapping.

abundant taxa, followed by trichopteran and anisopteran nymphs. After the sharp decrease in the number and biomass of these large invertebrates, the numbers of small aquatic invertebrates, such as cladocerans, increased in Pieni Majaslampi especially in 2006 and 2007 (Fig. 5).

Discussion

The substantial decrease in sulphur deposition since the end of the 1980s (Vuorenmaa 2004) has led to a large-scale decrease in sulphate concentrations and to an increase in alkalinity in acidified Finnish lakes, particularly in most affected areas in southern Finland (Mannio 2001, Forsius *et al*. 2003, Vuorenmaa and Forsius 2008). This chemical recovery pattern is also seen in the study lakes. Low pH associated with high concentrations of labile aluminium is considered essential for acidification-induced harmful effect in fish populations (Hultberg 1988, Rask *et al*. 1995). In our study lakes, the level of pH increased to > 5, and concentrations of labile aluminium decreased to < 100 μg l^{-1} during the 2000s, being below the critical limits in which perch populations are suggested to be strongly affected due to reproduction failures or deaths of adult fish (Rask and Tuunainen 1990, Rask *et al*. 1995). Tammi *et al*. (2004) reported that increases in pH and alkalinity, and decreases in labile aluminium concentrations are mainly responsible for a process of recovery of perch populations in acidified Finnish lakes. Episodic acidification — depression of pH and alkalinity and increase of aluminium concentrations during the springtime — also became less severe during the 2000s (Vuorenmaa 2007). This positive development has probably taken place in our study lakes, and has led to improved water quality and less acidic conditions during the spring-flow period, which is pre-requisite for successful reproduction of spring-spawning fish (Driscoll *et al*. 1980, Baker and Schofield 1982, Tuunainen *et al*. 1991).

Environmental factors other than reduced acid deposition also affect chemical and biological recovery from acidification in freshwaters (de Wit *et al*. 2007). According to the records of the Finnish Environment Institute, precipitation was very high in summer and autumn 2004 and in autumn 2006 (*see* www.ymparisto.fi/default.asp?contentid=128303&lan=en, www.ymparisto.fi/default.asp?contentid=225754&lan=fi&clan=en). This caused higher runoff and elevated leaching of humic material from the catchment, resulting in high amounts of organic acids entering the lakes. A significant fraction of the organic acids in the natural waters are strong organic acids (e.g. Munson and Gherini 1993). These organic acid surges may have reduced the alkalinity and pH and increased the aluminium concentrations in lakes in 2004 and 2006. Runoff-induced surges of organic acids can be an important factor suppressing recovery of pH and alkalinity in acid-sensitive Finnish lakes (Vuorenmaa and Forsius 2008). There is also another hydrology-induced possibility: ions may be diluted and runoff water may be less buffered due to accelerated water discharge from the catchment with shorter contact time between soil and water (Nuotio *et al*. 1990, Schindler *et al*. 1996).

Successful reproduction of perch during two and four summers in Hauklampi and Iso Majaslampi, respectively, suggests that the chemical recovery of the lakes has been sufficient enough to allow re-establishment of the perch populations in these lakes. However, seasonal and year-to-year variation in water quality and the morphometry of the lake (deep shoreline without proper breeding sites) seems to be critical, which is supported by the observed failure of the perch reproduction in Pieni Majaslampi, despite of its water quality being almost similar to that of the other two lakes during the autumn turnover. Hesthagen *et al.* (2001) tried to re-establish perch populations in some acidified lakes in southern Norway. The success of their attempt was low, apparently due to poor water quality (average pH 4.8 and labile aluminium even 140 $\mu g\ l^{-1}$) of the target lakes despite of their newly started process of chemical recovery.

The sharp increase in the growth of perch after their reintroduction to fishless lakes is a good example of the capability of perch to respond to changing conditions. Corresponding growth responses have been recorded for example after acid-induced decreases in perch densities (Raitaniemi *et al.* 1988, Nyberg *et al.* 1995) or after winter kill of fishes in eutrophic lakes due to oxygen deficit (J. Ruuhijärvi unpubl. data). The 6.5–7 cm average growth of perch in all three lakes in the first summer after stocking indicates that the stocked perch had good or even unlimited food resources. The faster growth of stocked perch in Iso Majaslampi in the second summer could be due to lower stocking density as compared with that in the other lakes or higher biological productivity of the lake. The highest invertebrate biomass in Iso Majaslampi before the perch stocking supports the latter assumption and so does the faster growth of lake-born perch, even if, as compared with Hauklampi, the sample consisted of few individuals only. In the lack of density estimates of lake-born perch there is also, however, the possibility that the perch year class of 2003 in Hauklampi was strong enough to result in intraspecific food competition and subsequent slower growth of perch.

Stomach content examination indicated only three cases where the stocked perch of Hauklampi had eaten some perch of the age group 1+ in 2004, but no evidence of 0+ eaten fishes was found, although cannibalism is known to be common in perch populations (Allen 1935, Horppila *et al.* 2000). Instead, stocked perch in our study lakes preferred benthic macroinvertebrates as perch often do in structurally simple habitats of small forest lakes (Rask 1983). Consequently, the sharp decrease in the numbers of actively moving invertebrates from the values before the fish releases was most probably a direct response to the predation after perch stocking. It is a clear example of a shift from invertebrate predator-dominated ecosystem of acidified fishless lakes (Eriksson *et al.* 1980, Rask *et al.* 2001) back to the dominance of fish as the top predator. The increased abundance of small macroinvertebrates in Pieni Majaslampi during the study period was probably caused by the failed reproduction of perch in that lake resulting in lower predation pressure on small prey. Presence of perch has also been found to strongly affect predatory invertebrates in more eutrophic habitats (Diehl 1992, Nummi *et al.* 2006).

Conclusions

The present trends in chemical variables that have direct toxic effects on biota (primarily pH and labile aluminium) are moving towards the levels tolerable for acid-sensitive fish species. Progressing chemical recovery of the study lakes has resulted in conditions that also enable biological recovery.

This experiment indicated, that reintroduced perch were capable of surviving and at least in some years of reproducing in lakes that earlier had lost their perch populations due to acidification. Thus, the results confirmed our hypothesis of improved conditions for perch as an effect of the chemical recovery of our experimental lakes during the 1990s and 2000s.

The strong initial growth response of reintroduced perch indicated favorable feeding conditions, which were based on high abundance of macroinvertebrates. Further, invertebrate predators were replaced by perch as the top predator of these lake ecosystems.

From the management point of view, reintroduction of fish into acidified lakes may speed up the process of recovery of the structure and function of these ecosystems and offer new possibilities of recreational fishing.

Acknowledgements: We thank Simo Jalli, Sami Vesala and others in Evo Game and Fisheries Research for catching perch, transporting and stocking them into the study lakes. Pekka Vanhala and Stefan Fronzek are thanked for helping in water chemistry sampling. Esa Pienmunne helped us in invertebrate trappings. Jeff Hearn revised the language. Kimmo K. Kahilainen and two anonymous referees gave constructive comments on the manuscript.

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