

Arctic charr (*Salvelinus alpinus*) re-established in a formerly acidified and highly dilute mountain lake under declining acidic deposition

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Arctic charr in Rondvatn, a formerly highly acidified mountain lake in southern Norway, was re-established through stocking. The population became extinct during the early 1980s when the lake had an annual mean pH of 5.2–5.4, with occasional declines to 4.3–4.7. From the mid to late 1990s, the pH and acid-neutralizing capacity (ANC) rose to 5.8–5.9 and 13–15 $\mu\text{eq L}^{-1}$, respectively. The lake is poor in ions with a mean conductivity and calcium concentration of 7.7 $\mu\text{S cm}^{-1}$ and 0.35 mg L^{-1} , respectively. The lake was stocked with 250 young Arctic charr from four small neighbouring lakes between 1998 and 2000. This introduction was successful. Test-fishing in 2004, 2008 and 2012 revealed a relatively dense population of Arctic charr, and the presence of several new age-groups. pH and ANC has remained stable since the late 1990s, or has slightly improved.

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INTRODUCTION

Acidification has brought widespread damage to fish populations in Nordic lakes (Rask *et al.* 2000; Tammi *et al.* 2003). In Norwegian lakes, brown trout (*Salmo trutta* L., 1758) have suffered the largest losses due to acidification (Hesthagen *et al.* 1999). Acidification may caused recruitment failure with high mortality rates of young fish (Schofield 1976; Harvey 1982). Some authors, however, have also suggested that old and mature fish can die in acidified waters (Rosseland *et al.* 1980; Mills & Schindler 1986).

Arctic charr (*Salvelinus alpinus* (L., 1758)) is the second most affected fish species in acidified watersheds in Norway, experiencing widespread declines at an early stage of the acidification process (Hesthagen & Sandlund 1995, Hesthagen *et al.* 1999). A number of studies on acidified Nordic lakes have shown that recruitment failure of Arctic charr appears to be the most frequent cause of population reductions and losses (Almer *et al.* 1974, Andersen *et al.* 1984, Hesthagen & Sandlund

1995, Hesthagen *et al.* 1995, 1998). Further, laboratory studies have confirmed that Arctic charr is an acid-sensitive fish species (Jagoe *et al.* 1984; Jones *et al.* 1985, 1987; Rosseland & Skogheim 1986).

Declining acid deposition across the northern hemisphere over recent decades is now highly evident (Tørseth *et al.* 2012). This has led to widespread improvements in water quality of formerly acidified waters (Skjelkvåle *et al.* 2005; Garmo *et al.* 2014). In a large number of Nordic lakes and rivers, water quality has also been improved through liming (Appelberg 1995; Sandøy & Romundstad 1995, Hesthagen *et al.* 2017).

Now there is a strong need to re-establish original fish communities in many of these formerly acidified waters. However, the natural colonization of fish assemblages after improved water quality due to reduced acidic deposition or liming, is restricted to factors such as closeness to existing populations and the possibilities of migration (cf. Appelberg 1998; Hesthagen *et al.* 2007). Natural colonization of some

species such as Arctic charr has failed because they lack existing populations within the watershed (Bergquist 1991). However, Arctic charr has been successfully re-introduced through stocking in limed Swedish lakes (Nyberg 1988). In fact, isolated lakes cannot be recolonised once a fish species has become extinct (Öhman *et al.* 2006). In Norway, re-introduction of fish species in lakes after improved water quality is to a large extent restricted to brown trout (Hesthagen & Østborg 2008; Hesthagen *et al.* 2011). This is because hatchery-reared brown trout are available for stocking, and brown trout is by far the most common fish species in Norwegian waters. Thus, donor populations may exist to re-populate empty lakes.

The aim of the present study was to assess the success of re-establishing Arctic charr in a formerly acidified mountain lake in southern Norway by means of stocking. We investigated relative population density, age and size distribution and occurrence of mature specimens. The development of Arctic charr after the introduction was related to several water chemistry variables, with emphasis on pH, inorganic toxic Al (Al_i) and acid-neutralizing capacity (ANC).

MATERIAL AND METHODS

Study area

The study was carried out in Lake Rondvatn, in Rondane mountain area, at an altitude of 1167 m a.s.l. (Figure 1). The watershed of the lake covers 20 km² of slowly weathering rocks such as granite and gneisses (Strøm 1944). The lake has a surface area of 0.96 km², and maximum depth is 56 m. A road leads to the lake, where there is a tourist cabin. Otherwise, the lake is not affected by local water pollution or habitat destruction.

Originally there was no fish present in Lake Rondvatn (Hesthagen 2009). In 1867, brown trout was introduced (Hetting 1871, Landmark 1877). In the 1890s, the lake was also stocked with Arctic charr (Sunde 1933). After the extinction of Arctic charr in the 1980s, there were multiple introductions of fish between 1998 and 2000. Arctic charr was caught with traps (1.5 x 0.5 m) in two small lakes (Illmanntjønnin) with better water quality, located in a sub-order branch about 1-3 km northeast of Lake Rondvatn. A total of 250 specimens, 10-15 cm in length and 1-2 years of age, were introduced. A very small population of brown trout has also been recorded in Lake Rondvatn in recent years, as one individual was caught during this study, in 2004.

Water chemistry

Water samples were taken close to the outlet of Lake Rondvatn on a near-monthly basis from 1980 to 2012. The annual number of samples ranged from 10 and 17, totally 432 samples. The parameters measured were pH, alkalinity, major ions (cations and anions), conductivity, phosphorous, nitrogen, aluminum species and total organic carbon (TOC), based on standard

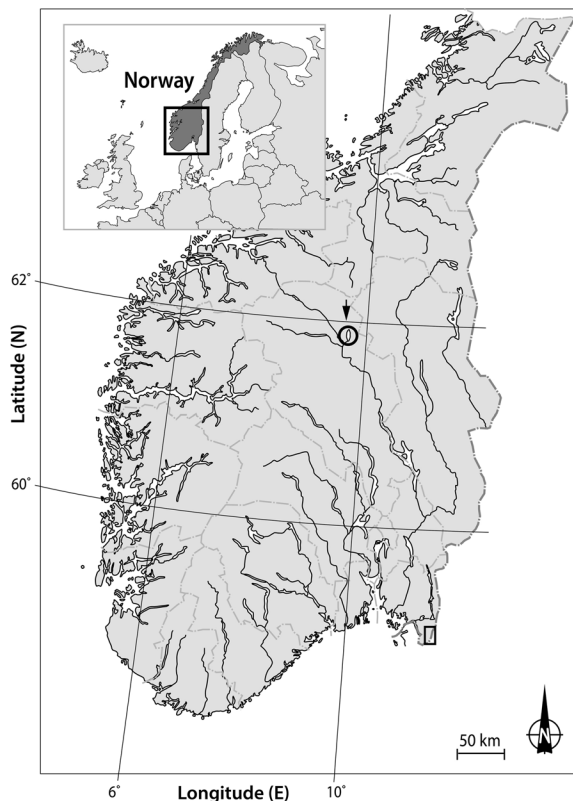


Figure 1. Map of southern Norway showing the location of Lake Rondvatn.

methods (cf. Garmo *et al.* 2014). Cations were determined by inductively-coupled plasma atomic-emission spectrometry (ICP-AES) and anions by ion chromatography until 1999. From 2000 these major ions have been analysed using HR-ICP-MS (high resolution-inductively coupled plasma-mass spectrometer). Different aluminum fractions were measured according to Eaton *et al.* (1995). Aluminum was not measured in 1984-1987. ANC was defined as the equivalent sum of base cations [$BC = Ca^{2+} + Mg^{2+} + K^+ + Na^+$] minus the equivalent sum of strong acid anions [$SAA = Cl^- + SO_4^{2-} + NO_3^-$] (Reuss & Johnson 1986). ANC could not be calculated in 1980-1986. The lake has very low concentrations of TOC, with a mean and \pm SD of 0.52 ± 0.33 mg L⁻¹. Thus, ANC was not modified by including permanent anionic charge of organic acids as part of the strong acid anions (cf. Lydersen *et al.* 2004).

Fish sampling

Fish were sampled with gillnets that were placed on the bottom (benthic) in August or early September in six different years between 1978 and 2012. The benthic gillnets used in 1978 and 1986 were 25.0 x 1.5 m, and one series consisted of eight nets with mesh sizes from 10 to 45 mm knot to knot (Rosseland *et al.* 1979). During this period, individual nets were placed from the shore line and down to depths of about 8-20 m. Since 1996, Nordic multi-mesh benthic gillnets were used during the test-fishing. Each gillnet was 30.0 x 1.5 m and consisted

of 12 mesh sizes from 5 to 55 mm knot to knot, and they were set throughout the lake in five different depth zones; 0-3, 3-6, 6-12, 12-20 and 20-35 m (cf. Appelberg *et al.* 1995). Pelagic gillnets of 54 x 6 m consisting of eight different mesh sizes from 10 to 45 mm knot to knot were used during the last four samplings (Rosseland *et al.* 1979). These nets were set at depths of 0-6 m and 6-12 m over the deepest part of the lake. All nets were set in the evening, and pulled in the following morning after about 12 hours fishing. The catch per unit effort (Cpue) is presented as number of fish caught 100 m⁻² net area night⁻¹. Data on total length (mm) and mass (g) were obtained from all fish (n=1030), while the degree of sexual maturity assessed by oocyte development was obtained from a subsample (n=407, 39.5%). Age determination was carried out using otoliths that were placed in 96% alcohol (Kristoffersen & Klemetsen 1991). A total of 413 specimens (40.1%) were aged.

RESULTS

Water chemistry

Lake Rondvatn has extremely dilute water with mean values \pm SD for conductivity and calcium concentration of 7.7 \pm 4.0 μ S cm⁻¹ and 0.35 \pm 0.33 mg L⁻¹, respectively (Table 1). The nutrient content is also very low with a phosphorous concentration of 2.5 \pm 0.8 μ g L⁻¹. There was a significant increase in pH throughout the study period, based on data from late autumn each year ($r^2=0.53$, $p<0.001$). The lake was highly acidified in 1980, with an annual mean pH of 5.2 (Figure 2). It remained acidified during most of the 1980s. pH ranged mainly between 5.2 and 5.4, with occasional declines to 4.3-4.7. In the early 1990s, the water quality improved, being most evident from

1994 to 1998 with a rise in pH and ANC to 5.8-5.9 and 13-15 μ eq L⁻¹, respectively (Table 1, Figure 2). The concentration of inorganic Al (Al_i) has been low since the measurements started in 1989, with mean annual values mainly between 5 and 11 μ g L⁻¹. Somewhat higher values were recorded in the mid-1990s with 14-16 μ g L⁻¹. Concentration of sulphur (SO₄) fell from an annual mean of 1.9 \pm 1.3 mg L⁻¹ in 1980 to 0.5 \pm 0.1 mg L⁻¹ in 2012.

Gillnets catches, and age and size distribution of Arctic charr

In 1978, the population of Arctic charr in lake Rondvatn was highly reduced with three fish caught 100 m⁻² net area night⁻¹ (Cpue) (Figure 3). In 1986 and 1996, no fish was caught during the test-fishing. In 2004, i.e. 4-6 years after the introductions, a dense population had already developed, with Cpue=38.5 on benthic gillnets. The Arctic charr population exhibited the same abundance in both 2008 and 2012 with Cpue of 43.8 and 40.7 specimens, respectively. Catches of Arctic charr in the pelagic nets were low, except for a somewhat higher catch in 2004 (Figure 3).

Arctic charr caught on benthic gillnets in 2004 ranged from 2 to 7 years, with age groups 1+ and 2+ being most abundant (Figure 4). A similar age distribution was found in both 2008 and 2012, except that older fish were more abundant, including some individuals at age 8+ and 9+. Arctic charr caught in the pelagic zone were significantly older than specimens from the benthic zone, with a mean age of 4.7 \pm 1.7 and 3.9 \pm 1.7 years, respectively. (two-independent-samples test: $F_{1,406}=26.26$, $p<0.005$). Fish length varied between 6 and 42 cm, of which 12-23 cm individuals dominated (Figure 5). Among fish > 20 cm, about 50% were mature.

Table 1. Mean values \pm standard deviation for 13 chemical variables from Lake Rondvatn, 1980-2012, grouped in periods of five years except for the first and last period with four years of data. * Not measured in that period. Tot-Al and Al_i is total and inorganic aluminum, respectively.

Variable	Unit	1980-1983	1984-1988	1989-1993	1994-1998	1999-2003	2004-2008	2009-2012
Cond.	μ S cm ⁻¹	7.4 \pm 4.3	7.7 \pm 2.0	9.0 \pm 4.0	7.0 \pm 2.9	8.2 \pm 5.9	6.9 \pm 3.4	7.4 \pm 4.1
pH		5.4 \pm 0.3	5.4 \pm 0.2	5.5 \pm 0.2	5.7 \pm 0.3	5.8 \pm 0.3	5.8 \pm 0.2	5.9 \pm 0.3
Alkalinity	μ eq L ⁻¹	12.7 \pm 13.4	3.8 \pm 5.1	4.8 \pm 7.3	10.3 \pm 13.4	16.6 \pm 21.1	11.2 \pm 13.4	22.0 \pm 22.2
Ca	Mg L ⁻¹	0.4 \pm 0.2	0.4 \pm 0.1	0.4 \pm 0.1	0.3 \pm 0.1	0.3 \pm 0.2	0.3 \pm 0.1	0.3 \pm 0.2
Mg	Mg L ⁻¹	0.1 \pm 0.1	0.1 \pm 0.1	0.1 \pm 0.1	0.1 \pm 0.0	0.1 \pm 0.1	0.1 \pm 0.0	0.1 \pm 0.1
Na	Mg L ⁻¹	0.3 \pm 0.2	0.3 \pm 0.2	0.4 \pm 0.4	0.3 \pm 0.1	0.4 \pm 0.3	0.4 \pm 0.4	0.3 \pm 0.3
K	Mg L ⁻¹	0.4 \pm 0.2	0.4 \pm 0.1	0.4 \pm 0.1	0.4 \pm 0.2	0.5 \pm 0.3	0.5 \pm 0.3	0.4 \pm 0.3
SO ₄	Mg L ⁻¹	1.8 \pm 0.6	1.2 \pm 0.2	1.1 \pm 0.4	1.0 \pm 0.4	0.8 \pm 0.3	0.6 \pm 0.1	0.6 \pm 0.2
Cl	Mg L ⁻¹	0.3 \pm 0.4	0.3 \pm 0.3	0.6 \pm 0.6	0.4 \pm 0.2	0.5 \pm 0.6	0.5 \pm 0.6	0.5 \pm 0.4
NO ₃	μ gN L ⁻¹	*	167 \pm 60	171 \pm 69	114 \pm 82	126 \pm 70	150 \pm 39	158 \pm 57
Tot-Al	μ g L ⁻¹	58 \pm 17	60 \pm 29	42 \pm 26	47 \pm 41	42 \pm 63	35 \pm 12	42 \pm 24
Al _i	μ g L ⁻¹	*	*	9 \pm 9	11 \pm 15	6 \pm 6	5 \pm 5	6 \pm 7
ANC	μ eq L ⁻¹	*	-8 \pm 9	-0 \pm 10	1 \pm 15	12 \pm 14	10 \pm 12	11 \pm 22

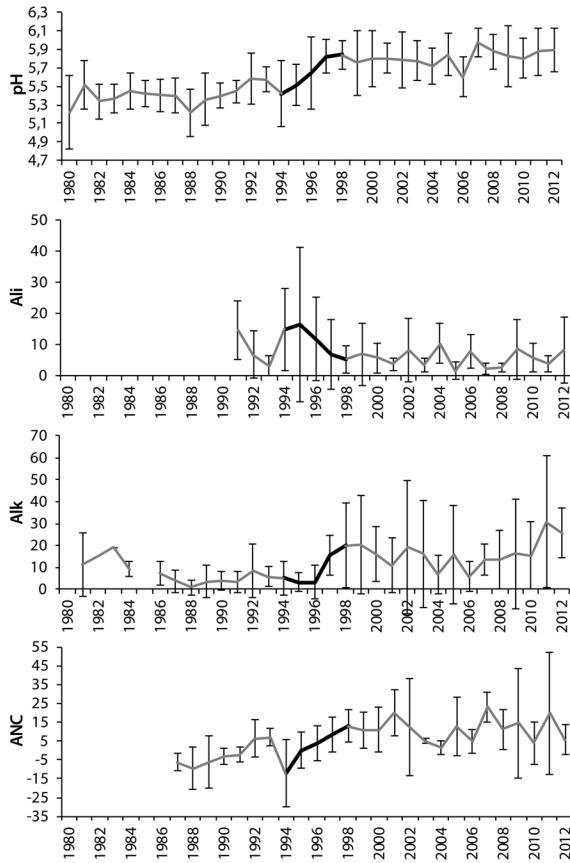


Figure 2. Yearly average pH, inorganic Al (Al_i), alkalinity (Alk) and ANC from Lake Rondvatn between 1980 and 2012. Data is not available for some of the years. Years with the most pronounced improvement in water quality (1994-1998) are highlighted with bold lines.

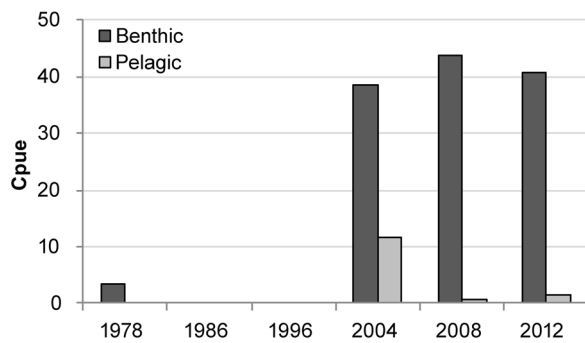


Figure 3. Catches of Arctic charr expressed as number of fish caught 100 m² net area night⁻¹ (Cpue) in benthic and pelagic gillnets in Lake Rondvatn in 1978, 1986, 1996, 2004, 2008 and 2012.

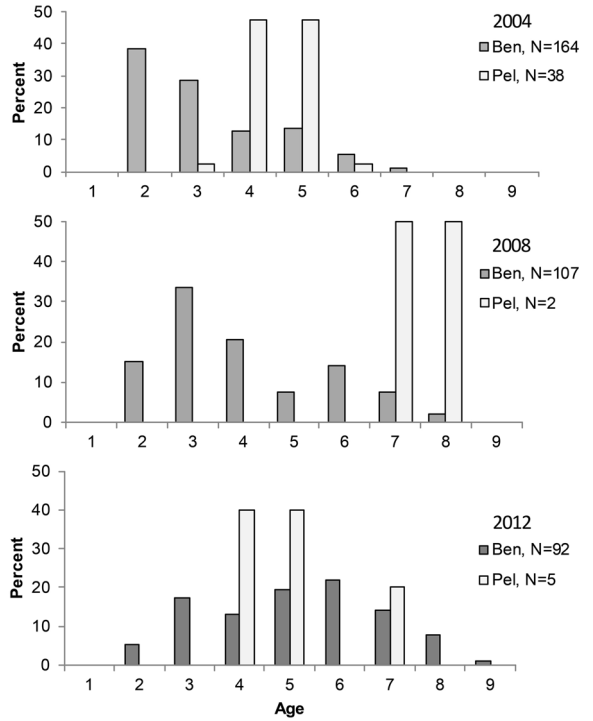


Figure 4. Age distribution (percent) of Arctic charr caught by benthic (Ben) and pelagic (Pel) gillnets in Lake Rondvatn in 2004, 2008 and 2012. N=number of fish aged.

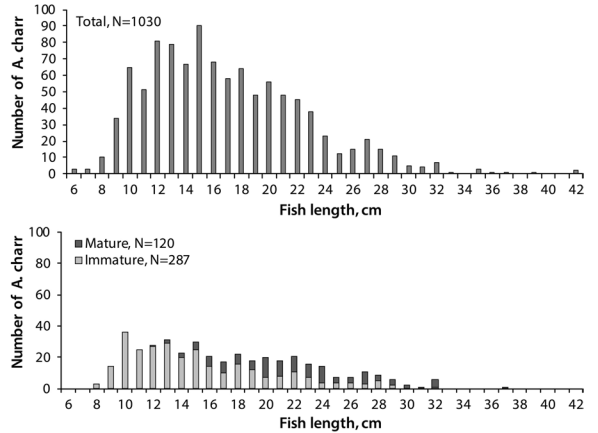


Figure 5. Length frequency distribution of total number of Arctic charr (top) and that of a subsample where mature and immature specimens are differentiated in gillnets catches from Lake Rondvatn in 2004, 2008 and 2012. N=number of fish.

DISCUSSION

Lake Rondvatn was probably not seriously acidified as early as in 1928–1941, when pH ranged between 6.0 and > 8.4 (Strøm 1944; Wright 1977). These values were based on colorimetric measurements, and are not directly comparable with ours. However, a study carried out between March and July 1974 showed that Lake Rondvatn was by then acidified, with pH mostly ranging between 5.4 and 5.8 (Dovland 1975). Arctic charr in Lake Rondvatn must have been started to decline in the 1960s, as only a few specimens were caught in 1978. Thus, the lake must have been acidified to some extent at that time. The population of Arctic charr probably became extinct during the early 1980s. At that time, the lake had an annual mean pH of 5.2–5.4, with occasional declines to 4.3–4.7. ANC was mainly negative until 1992, ranging mostly between -1 to -10 $\mu\text{eq L}^{-1}$. In such water, Arctic charr are expected to be severely damaged (Hesthagen & Sandlund 1995; Lien *et al.* 1996). However, the water quality improved significantly from the mid 1990s until 1998, with pH=5.8, alkalinity=20 $\mu\text{eq L}^{-1}$, ANC=13 $\mu\text{eq L}^{-1}$ and inorganic Al=5 $\mu\text{eq L}^{-1}$. Thus, water quality should no longer limit Arctic charr abundance in Lake Rondvatn (cf. Hesthagen & Sandlund 1995).

The concentration of inorganic Al in Lake Rondvatn was low with maximum values in the early 1990s of 14–16 $\mu\text{g L}^{-1}$. A nation-wide survey of Norwegian lakes found that pH and inorganic Al were the two most significant variables explaining the variability in community status of Arctic charr, based on data from 349 lakes (Hesthagen & Sandlund 1995). Lakes with damaged and extinct populations of Arctic charr had mean values of inorganic Al of 48 and 83 $\mu\text{g L}^{-1}$, respectively. The extinction of Arctic charr in Lake Rondvatn may be due to its extremely dilute water, with a mean conductivity and calcium concentration of 7.7 $\mu\text{S cm}^{-1}$ and 0.35 mg L^{-1} , respectively. It has recently been shown that ion deficit restricts the distribution of brown trout in slightly acidic mountain lakes in southernmost Norway (Enge & Hesthagen 2016). These lakes had a median conductivity and calcium concentration of 8.7 $\mu\text{S cm}^{-1}$ and 0.23 mg L^{-1} , respectively (Enge 2013). The effects of ion deficit are probably associated with some physiological disruptions, as passive loss of ions to the water needs to be compensated by active uptake of ions from the environment (cf. Heath 1995).

Arctic charr caught in Lake Rondvatn in 1978 ranged between 13 and 25 years of age (Sevaldrud & Muniz 1980). This strongly suggests that the population suffered from recruitment failure. The re-established population during the early 2000s displayed a normal age distribution in terms of abundance of young fish and occurrence of mature and older specimens. Thus, recruitment failure or maturation-induced mortality no longer appear to exist (cf. Rosseland *et al.* 1980; Frenette & Dodson 1984; Mills & Schindler 1986; Trippel & Harvey 1987).

Arctic charr in Lake Rondvatn were re-established based on fish introduced from four small lakes in a sub-order branch of the watershed. In most cases, introductions by humans

seems to be necessary to re-establish Arctic charr in previously acidified lakes in Norway. This is the case also for other fish species that were lost during recent decades except for brown trout (cf. Hesthagen & Østberg 2008). This is due to lack of donor populations in upstream areas, or physical barriers in other parts of the watershed where that species might exist (Appelberg 1998; Hesthagen *et al.* 2007). Thus, most of the nearly 1500 populations of other fish species that were lost due to acidification remain to be re-established (cf. Hesthagen *et al.* 1999).

Lake Rondvatn had probably no fish when the stocking of Arctic charr started in 1998, maybe except for a small population of brown trout. Thus, the introduction of Arctic charr could have been more likely to be successful due to this fact. However, the lake was densely populated with Arctic charr in several decades prior to the acidification process, and brown trout has always been rare. This is probably mainly because Arctic charr outcompete brown trout in deep, oligotrophic lakes (cf. Finstad *et al.* 2011). These conditions characteristic of Lake Rondvatn in both aspects. However, the spawning conditions for brown trout in this lake is considered to be limited.

We conclude that the decline and extinction of Arctic charr in Lake Rondvatn was due to acidification as shown by low pH and ANC. This occurred in spite of low levels of inorganic Al, probably due to highly dilute water. No other factors, such as environmental perturbation or habitat encroachment have probably extinguished Arctic charr in the lake. The population of Arctic charr and brown trout in Lake Atnsjøen, which is located about 14 km east of Lake Rondvatn, may be used as a reference. However, no large changes in their abundance or age structure have been found between 1985 and 2012 (Hesthagen *et al.* 2004; Saksgård & Hesthagen 2004, 2014). Lake Atnsjøen is not regarded as acidified, with a pH of about 6.0 (Halvorsen 2004). Although the water quality in most lakes where Arctic charr have been lost due to acidification is now probably sufficient for re-establishing the species, physical barriers or lack of potential donor populations available for re-introduction hinder re-establishment. Thus, re-establishing this salmonid species in such lakes will largely rely on human introductions.

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