Reduced acid deposition leads to new start for brown trout (*Salmo trutta*) in an acidified lake in southern Norway

Espen Lund, espen.lund@niva.no, corresponding author, phone +47 47400858, ORCID 0000-0003-4089-9068

Øyvind A. Garmo, oyvind.garmo@niva.no

Heleen A. de Wit, heleen.de.wit@niva.no, ORCID 0000-0001-5646-5390

Torstein Kristensen, torstein.kristensen@nord.no, ORCID 0000-0002-2640-4260

Kate L. Hawley, kate.hawley@niva.no

Richard F. Wright, richard.wright@niva.no

A Norwegian Institute for Water Research (NIVA), Gaustadalléen 21, 0349 Oslo, Norway.

B Nord University, Universitetsalléen 11, 8026 Bodø, Norway.

C Current: Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, 1432 Ås, Norway. kate.louise.hawley@nmbu.no

Keywords: acidification, acid neutralising capacity, fish, recovery

Acknowledgements

The long-term data series at Langtjern would not have been possible without the enthusiastic and dogged efforts of our emeritus colleagues Arne Henriksen, Magne Grande, and Sigbjørn Andersen and the local help of Kolbjørn Sønsteby.
Abstract

Acid deposition has led to acidification and loss of fish populations in thousands of lakes and streams in Norway. Since the peak in the late 1970s acid deposition has been greatly reduced, and acidified surface waters have shown chemical recovery. Biological recovery, in particular fish populations, however, has lagged behind. Long-term monitoring of water chemistry and fish populations in Lake Langtjern, south-eastern Norway, show that around 2008 chemical recovery had progressed to the point at which natural reproduction of brown trout \textit{(Salmo trutta)} reoccurred. The stocked brown trout reproduced in the period 2008–2014, probably for the first time since the 1960s, but reproduction and/or early life stage survival was very low. The results indicate that chemical thresholds for reproduction in this lake are approximately pH = 5.1, Al$_i$ = 26 µg/l, ANC = 47 µeq/l, and ANC$_{oaa}$ = 10 µeq/l as annual mean values. These thresholds agree largely with the few other cases of documented recovery of brown trout in sites in Norway, Sweden and the UK. Occurrence and duration of acidic episodes have decreased considerably since the 1980s, but still occur and probably limit reproduction success.
Introduction

During the 20th century acid deposition caused environmental damage in large regions of Europe and eastern North America. In Norway, thousands of lakes and streams were acidified, with the resultant loss and damage to freshwater fish populations (Hesthagen et al. 1999). Southern Norway is particularly vulnerable to acid deposition due to the highly siliceous and weathering-resistant bedrock and overburden, and thin and patchy organic-rich soils (Wright and Henriksen 1978). Acid deposition in Europe peaked in the late 1970s and has declined sharply over the past 30 years (Schöpp et al. 2003), largely as a result of implementation of international agreements to reduce the emissions of acidifying air pollutants (UNECE 2014). Acidified freshwaters in Norway have shown dramatic improvements in water chemistry as a response to declining acid deposition (Skjelkvåle et al. 1998; Garmo et al. 2014; Gray et al. 2016). In many cases, however, biological recovery has lagged behind chemical recovery (Hesthagen et al. 2011; Hesthagen et al. 2016).

Damage to salmonid fish populations, in particular the brown trout (Salmo trutta), in acidified lakes is usually due to recruitment failure. The eggs and young fry are the most sensitive life stages, and they are often exposed to the acidic water during snowmelt (Overrein et al. 1980; Serrano et al. 2008). In marginally-acidified lakes stocking with young fish may be successful, but reproduction often fails. Toxicity is largely due to elevated concentrations of inorganic aluminium species (termed here Al₃) (Baker and Schofield 1982; Rosseland et al. 1990). Toxicity of Al₃ is ameliorated by dissolved organic carbon (DOC) in the water through formation of Al-humus complexes (Cronan et al. 1986).

Al₃ is mobilized from soils by acidic water. The strong acid anions sulphate (SO₄) and nitrate (NO₃) in acid deposition acidify the soil and mobilize Al₃ (Reuss et al. 1990). Acid neutralising capacity (ANC), defined as the equivalent sum of the concentrations of base cations minus the equivalent sum of the concentrations of strong acid anions, is commonly used as a measure of the acidification of freshwaters (Reuss et al. 1987). There was a close relationship between ANC and the brown trout
population status in lakes in Norway during the 1980s when acidification was near its peak (Lien et al. 1996). Inclusion of organic strong acids (ANC$_{oaa}$; "organic acid adjusted") slightly improved the correlation (Lydersen et al. 2004).

Documentation of chemical and biological recovery in acidified lakes requires systematic long-term monitoring. In southern Norway, Lake Langtjern is one such monitoring site where water chemistry and fish populations have been monitored since the 1970s (Henriksen and Wright 1977; Henriksen and Grande 2002; De Wit et al. 2014). The native brown trout population disappeared around 1960, probably because of acidification (Henriksen and Grande 2002). pH in the lake was generally below 5.0 in the 1970s. Since then, the lake has been stocked several times for research purposes with brown trout, brook trout (Salvelinus fontinalis) and rainbow trout (Oncorhynchus mykiss) to study the relative tolerance of various fish species to acid water (Grande et al. 1978). The stocking did not result in natural reproduction in the lake, until recent findings of small, non-stocked brown trout.

Here we investigate the recent fish recovery in relation to changes in the water chemistry of Lake Langtjern over the 42-year period 1973–2014.

Materials and methods

The catchment and the lake

Lake Langtjern (https://www.niva.no/en/services/environmental-monitoring/langtjern) is a small, headwater lake located in Flå township, Buskerud county, about 75 km north of Oslo, southeastern Norway (Fig. 1). Lake Langtjern has been a site for monitoring and research on acidification since 1972. It is undisturbed from direct human influence and has never been limed. The lake and its catchment are included in several national and international monitoring programs. The lake is 0.23 km$^2$ with catchment including the lake 4.7 km$^2$. The lake is relatively shallow, with maximum depth 12 m and mean depth 2 m. The catchment is mixed sparse forest of pine, spruce and birch. Soils are
thin and organic-rich podsols developed on weathering-resistant glacial moraine and bedrock of
gneisses and granites. The catchment is 63 % forest, 16 % peatland and 16 % exposed bedrock. Apart
from a minor amount of forest harvesting, there is no other human disturbance or sources of
pollution to the lake or the catchment. The lake and its catchment including exclusive fishing rights
have been leased to the Norwegian Institute for Water Research for research and monitoring
purposes since 1973.
The lake has three inflowing streams; only the largest of these (LAE02) and the outlet
(LAE01) provide suitable habitat as spawning beds for trout. The width of the outlet stream is 1–2 m.
The outlet has two dam constructions: an old large stone dam previously used to float timber and a
newer concrete dam downstream with v-notch weir installed in 1973 for measuring discharge. The
older stone dam restricts free water flow when discharge is large and has an opening at the bottom
which allows fish passage both ways at all levels of water discharge. The v-notch weir has a waterfall
that effectively prevents any upstream migration of fish. From the lake outlet, it is about 30 m to the
stone dam and 100 m to the concrete dam. The main inlet (LAE02) has a width of about 0.5–1 m.
Both streams have sections of shallow water, but also some deeper pools. The substrate varies from
fine to coarse. Suitable brown trout spawning substrates are more common in the inlet (LAE02) than
in the outlet.
Deposition data

The nearby stations Brekkebygda (1998–2015) and Gulsvik (1974–1997) are part of the national atmospheric monitoring programme run by the Norwegian Institute for Air Research (NILU).

Bulk deposition is collected in weekly samples, and volume and concentrations of major ions measured at NILU and reported annually (Aas et al. 2016).

Discharge data

Langtjern is a station in the national hydrology monitoring programme run by The Norwegian Water Resources and Energy Directorate (NVE). Discharge is measured continuously by water-level recorder at the v-notch weir. The data are reported as mean daily discharge.

Water chemistry data

Samples for water chemistry have been collected weekly from the outlet since 1973, except during an 18-month period with no funding in 1984–1985. Water chemistry parameters relevant to acidification have been analysed; these include major cations and anions, aluminium species (from 1986), and dissolved organic carbon (from 1986). The inlets and the lake itself have also been sampled, but not as frequently or as systematically as the outlet. The monitoring data and analytical methods used are reported annually (Garmo et al. 2016).

Fish data

Fish catch and stocking information for the period 1906–1971 was derived from log books kept by the local fishermen and other anecdotal information from local people. Beginning in 1972, experimental fish stockings and gill net catches were systematically recorded (Henriksen and Grande 2002). During the period 2000–2003, investigations were conducted to assess the potential for natural recruitment of brown trout in the lake. In autumn 2000, 216 fertilized brown trout eggs of the Nordmarka (Oslo) strain were placed at potential spawning sites in the outlet (72 eggs in 3 boxes) and main inlet (144 eggs in 6 boxes) and then inspected periodically for survival rates to
hatching in May 2001. In September 2002, the streams were sampled by electrofishing with a
backpack apparatus (Bohlin et al. 1989). In August 2003, the lake was sampled by 9 multi mesh
survey nets of 32 m and 4 single mesh nets of 25 m with mesh widths 10 mm, 12.5 mm, 16 mm and
22 mm.

In August 2010, October 2011, October 2012, August 2013 and August 2014, the outlet and
main inlet were sampled by one or two passes of electrofishing, except 2014 when only outlet was
sampled. The outlet stream was sampled in an area of ca. 150 m², covering the full width of the
stream from the outlet down to the V-notch weir about 100 m downstream. The inlet was sampled
in an area of ca. 130 m², covering the full width of the stream from the lake to about 130 m
upstream. Length and weight of the captured fish were measured, and the fish then released into
the same stream. Young-of-the-year (age 0+) were counted to assess the year specific reproduction.
This age class was separated from older classes (>0+) mainly by fish lengths, but also by reading
scales samples of some individuals. Gender and sexual maturation were determined only when
possible.

Statistical methods

We analysed for break points in the various data series by means of the software package
Change-Point Analyzer ver. 2.3 (Taylor Enterprises, Inc.), where annual means were analysed for
significant changes with 95 % confidence level using 1000 bootstraps without replacements. In some
series, data were grouped to avoid violation of the assumptions of independent errors.

Duration of extremes was estimated by counting days between consecutive measurements
of extreme values, assuming the values to be extreme in the period between the actual
measurements. We used the thresholds of ANC 10 µeq l⁻¹, ANC₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉¢⁻¹, pH 4.8 and Al₅₀ µg l⁻¹.
Days between two consecutive measurements were counted if both measured values were below
the thresholds for ANC, ANC₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉₉¢⁻¹ or pH and above the threshold for Al₅₀. Measurements were weekly
and the expected count between two such values was therefore seven.
Results

Water chemistry

The concentrations of $SO_4$ in the outlet have decreased sharply since the peak years in the 1970s (Fig. 2). This has been in response to the large decrease in $SO_4$ deposition – from about 40 meq m$^{-2}$ yr$^{-1}$ in the late 1970s to about 10 meq m$^{-2}$ yr$^{-1}$ in the 2010s (Fig. 2). The large decrease in $SO_4$ deposition from 1991 to 1997 corresponds to the decrease in $SO_4$ concentrations in the outlet from 1993 to 2000, with a delayed response of less than two years (Table 1) (Fig. 2). The decreasing concentrations of $SO_4$ in the outlet have been accompanied in part by lower concentrations of base cations such as Ca, and in part by higher pH and lower concentration of Al. The ANC and ANC$_{oaa}$ have increased, and the water has become less toxic to fish (Table 1). At Langtjern concentrations of nitrate (NO$_3$) are in the range 1–2 µeq l$^{-1}$, showing lower values in recent decades. Thus nitrogen deposition plays a minor role relative to sulphur in surface water acidification at this site. TOC has increased since the mid 1980s, which is the reason for the slight decline in ANC$_{oaa}$ in the period 2008–2014.

The 42-year record of annual $SO_4$ deposition and mean concentrations of $SO_4$, Ca, ANC, ANC$_{oaa}$ and pH in the outlet had change-points during 1997–2001, with decreased $SO_4$ deposition, $SO_4$ and Ca and increased ANC, ANC$_{oaa}$ and pH (Fig. 2). A second change point was found in 1991–1992. The change-points for ANC and ANC$_{oaa}$ in 2000 had confidence intervals which included 2002 and 2001, respectively. The decrease in $SO_4$ of 41 µeq l$^{-1}$ was associated with a decrease of Ca of 11 µeq l$^{-1}$ and an increase of ANC of 28 µeq l$^{-1}$.

The occurrence and duration of acidic episodes have decreased considerably since the 1980s (Fig. 3). During 1973–1992 in the Langtjern outlet, there were many periods of more than 90 consecutive days of pH < 4.8. Before 1995 it was usual to have more than 14 days of pH < 4.8 every year. Then, in the period 1996–2014, there were 11 years without consecutive weekly measurements of pH < 4.8. Periods of Al $>$ 50 µg l$^{-1}$ were more frequent and much longer before
196 1995 than after. Since 1995, only two years had high Al periods of 14 days or more. Periods of ANC <
197 10 µeq l⁻¹ were more frequent and of much longer duration before 1990 than after. After 1990, only
198 three years had such periods: 1991, 1994 and 2000. For ANC_\text{oaa} < -5 µeq l⁻¹, there were fewer and
199 shorter periods after year 2001.
200
201 Fish
202 According to anecdotal information from the local fishermen and log books on fish catches in
203 Lake Langtjern, the lake lost its population of brown trout during the 1960s, probably due to
204 acidification. This “original” population was a result of several stockings of brown trout since ca.
205 1906 and the natural offspring of these. Gill net catches were relatively good for the first decades of
206 the 1900s, but then very poor in 1967–1969. From 1972, the lake was managed for research
207 purposes and repeatedly stocked with brown trout and also brook trout usually aged 1+ (Fig. 4)
208 (Henriksen and Grande 2002). The last stocking was of 400 brown trout in June 2006. There was no
209 systematic tagging of the stocked fish, but most were fin clipped. The stocked fish were also
210 captured (and killed), usually by use of gill nets each summer, with the last gill net catch conducted
211 in 2011. The gill net catches usually corresponded to the previous stocking of fish, i.e. the stocked
212 fish were recognized (by size and fin clippings) in the catches some 2–4 years after release (Fig. 4).
213 Captured fish were mainly marked (fin clipping) confirming recaptures of stocked fish. Unmarked
214 captures, which could be wild or stocked, were very rare and did not point to an ongoing natural
215 reproduction. During the period 1992–2000, recapture of stocked fish was estimated to 20%
216 (Henriksen and Grande 2002). The remaining 80% of the stocked fish usually disappeared after 6–8
217 years, presumably owing to natural causes, but possibly as a result of the acidification. There usually
218 were mature individuals among the captured fish. Probably, there have been mature fish in the lake
219 in varying numbers since the 1970s, but the gill net captures have not indicated any successful
220 reproduction of trout.
The studies of possible trout recruitment starting in the winter 2000-01 gave negative results. In May 2001, all eggs in the experimental boxes in the substrate were dead when inspected. At the same time, dead eggs from natural spawning were also observed. The September 2002 electrofishing resulted in no catches in the streams. The August 2003 lake sampling by gill nets gave no catch of non-stocked fish. Studies were resumed in 2010, and for the first time recruitment of young brown trout was observed. The electrofishing in the outlet (LAE01) and the major inlet (LAE02) in 2010–2014 resulted in captures of non-stocked brown trout each year (Table 2). These fish were not fin clipped, and they were much smaller than the expected size of the stocked fish from 2006. In 2011, 2012 and 2014 there were electrofishing catches of young-of-the-year brown trout, with fish lengths < 8 cm in August catches and < 9 cm in October. Mature individuals of both sexes, and of both wild (< 27 cm, n=3) and stocked origin (> 38 cm, n=2), were captured in the outlet in 2011 and 2012.

Discussion
The chemical recovery at Langtjern follows the well-documented pattern seen in acidified lakes and streams in many parts of Europe and eastern North America (Stoddard et al. 1999; Jeffries et al. 2003; Skjelkvåle et al. 2007; Futter et al. 2014; Monteith et al. 2014; Rask et al. 2014; Driscoll et al. 2016). The reduced deposition of SO$_4$ has led to lower concentrations of SO$_4$ in surface waters. pH and ANC have increased while Al$_i$ has decreased. In addition, TOC has increased, which is a result of increasing organic matter solubility related to lower electrolyte concentrations and reduced acidity (De Wit et al. 2007). Also, concentrations of NO$_3$ decreased, probably as a combined result of climate warming (less snow cover) and lower N deposition (de Wit et al. 2008).

The lag time of <2 years between reductions in SO$_4$ deposition and decrease in concentrations of SO$_4$ in the lake observed at Langtjern is also not unexpected, as soil processes such as adsorption and desorption of SO$_4$ are minor in young, organic-rich soils such as those at Langtjern (Reuss and Johnson 1986). The in-lake processes that also act to dampen changes in SO$_4$
concentrations are also apparently of minor importance relative to the through-flux of SO$_4$ in the lake (Couture et al. 2016).

The fish catches indicate an important qualitative change in the brown trout ecology in Lake Langtjern: the stocked fish now reproduce, *albeit* to a very low extent and maybe not every year. Thus, water quality in the outlet and inlet streams is apparently close to a critical limit for successful brown trout reproduction.

The exact year of the first successful reproduction in recent times cannot be ascertained, but we know from the electrofishing that young-of-the-year brown trout were produced in 2011, 2012 and 2014 (Table 2). The estimated age of older captured fish suggests that brown trout reproduced also in 2008 and 2009. Gill net sampling, electrofishing and egg exposure experiments indicate that reproduction probably did *not* occur in 2001 and 2002. The August 2003 gill net sampling in the lake would not have been able to capture potential young-of-year, as they would have been residing in the stream; thus there are no data on the trout reproduction in 2003. Hence, the first successful reproduction was probably in the period 2003–2008.

Langtjern is one of a few acid water monitoring sites in Norway at which long-term data record the recovery of the brown trout following reductions in acid deposition. Hesthagen et al. (2011) have documented the revitalisation of the brown trout population in Lake Saudlandsvatn, southernmost Norway. Here the native population was severely depleted, but never completely lost, and was able to naturally reproduce when water quality improved in the 1990s. Similarly, brown trout recruitment became increasingly successful in streams in the River Vikedal catchment (Hesthagen et al. 2001) during the 1990s, *albeit* with occasional setbacks due to acidic episodes (Hesthagen et al. 2016).

There are only a few documented cases of recovery of fish populations from acidified waters elsewhere in Europe and eastern North America. This appears to be because of the paucity of long-term data monitoring fish populations, but perhaps also because of factors acting to delay biological recovery in response to chemical recovery. In Sweden, the thousands of acidified lakes have shown
Chemical recovery since the 1980s (Futter et al. 2014), but there are apparently few lakes in which the long-term data are sufficient to document recovery of fish populations (Holmgren 2014). Valinia et al. (2014) found that in a dataset of 28 Swedish lakes, the roach (*Rutilus rutilus*) population had been lost in 14 lakes due to acidification in the 1980s, but in 2010 it had reappeared in 5 of these in response to chemical recovery. In Finland there has been widespread recovery of perch (*Perca fluviatilis*) populations, but the more acid-sensitive roach shows much less recovery (Rask et al. 2014). In the United Kingdom two of the 22 sites in the acid waters monitoring network (AWMN) now show recovery of brown trout populations (Malcolm et al. 2014) in response to the general improvement in water quality due to reduced sulphur deposition (Monteith et al. 2014). In the eastern United States long-term monitoring data from 43 lakes in the Adirondack Mountains, New York, show reduced acidity in response to decreased sulphur deposition, but so far there have been no major improvements in populations of brook trout (Baldigo et al. 2016). Likewise in eastern Canada there have been several reports of improved fish populations in acidified lakes and streams of Atlantic Canada (Lacoul et al. 2011) and in acidified lakes near Sudbury, Ontario (Gunn and Keller 1990, Snucins et al. 2001).

Chemical recovery proceeds along a continuum, whereas biological recovery is often marked by thresholds. There have been many studies of the tolerance of fish species to acidified waters, in particular the brown trout. Empirical data for water chemistry and brown trout populations from synoptic surveys of 1000 lakes in Norway show that there were rather sharp thresholds of ANC for the transition between “not affected” and “reduced” populations, and between “reduced” and “extinct” populations in the 1980s (Bulger et al. 1993, Lien et al. 1996). Fitting a logistic expression to the data explained 54% of the variance. Including organic acids in the expression for ANC increased the strength of these relationships to 56% (Lydersen et al. 2004). ANC is particularly appropriate in humic lakes, such as Langtjern. A threshold for ANC of 8 µeq/l gave a 95% probability for no population damage to brown trout in Norwegian lakes based on the survey data from 1986.
Hesthagen et al. (2008)) revisited these thresholds based on a new survey of the Norwegian lakes conducted in 1995. Their analysis indicates that in 1995 the threshold for 95% probability for no population damage to brown trout was ANC$_{oaa}$ 48 µeq/l, substantially higher than the value for the 1986 data. They suggest that the higher ANC$_{oaa}$ threshold found for the 1995 data might be caused by a lower pH and a higher Al$_i$ concentration at a given ANC value in 1995 than in the 1980s. But this difference could also be caused by the lag times between changes in water chemistry and population status in lakes.

Based on the long-term field data from the streams in the River Vikedal catchment, Hesthagen et al. (2016) suggest that recruitment of brown trout can give low density of fry at ANC$_{oaa}$ levels of -18 to -5 µeq l$^{-1}$, increased but unstable densities at ANC$_{oaa}$ -5 to +10 µeq l$^{-1}$, and steady increase in density at ANC$_{oaa}$ above 10 µeq l$^{-1}$. They indicate that ANC$_{oaa}$ of 20–25 µeq l$^{-1}$ is necessary for significant recovery of young brown trout in streams. This value is consistent with the observed fish recovery at Lake Saudlandsvatn (Hesthagen et al. 2011). The UK data of Malcolm et al. (2014) indicate threshold value of ANC$_{oaa}$ in the range 7 to 38 µeq l$^{-1}$, for 80% probability of brown trout fry present in two of three sampled stream reaches.

The data from Langtjern fit this picture. For the period 2008–2014 during which reproduction occurred, the outlet water chemistry mean values of ANC$_{oaa}$ was 10 µeq l$^{-1}$ (Table 1), the threshold indicated by Hesthagen et al. (2016)) for unstable densities of young brown trout in running water. Further, the mean values for 2008–2014 were similar to the mean values for 2000–2007, suggesting that the conditions were close to the critical limits also prior to 2008.

The ANC in Lake Langtjern is not likely to further increase appreciably soon. There is little room for further reductions in SO$_4$ deposition as levels in 2015 were only 7% of those in the peak year 1980 (Aas et al. 2016). Nitrate makes only a minor contribution to ANC and appears to be declining (De Wit et al. 2008). Thus any major increase in ANC will have to come from increasing concentrations of base cations caused by replenishment of soil base cation pools due to natural weathering, a process that typically takes decades (Hodson and Langan 1999). ANC$_{oaa}$, on the other
hand, could increase with a decline in TOC. ANCoaa is the organic acid adjusted ANC, where organic acids (TOC) are subtracted from the base cation concentration to give an adjusted, and reduced, ANC. However, TOC concentrations do not show any sign of levelling off and may increase further under a wetter climate (de Wit et al. 2016).

The change-points for ANC and ANCoaa in 2000 may explain why the successful reproduction of brown trout started at some point after 2002. Although the estimated change-point in 2000 does not fit with the different investigations indicating no reproduction during 2001–2002, the confidence interval for the ANC change-point was 2000–2002, and the upper limit makes it possible that the positive change in ANC level occurred shortly after the known period of non-successful reproduction. The 1997 change-point in SO₄ indicates that the reduced SO₄ concentration was the main cause for the ANC upward change, although the two changes were not estimated to occur at the same time.

ANC is a convenient measure of lake acidification. Toxicity to fish, however, is caused by Al₃ and/or H⁺. The recent reproductive success might better be explained by lower frequency, severity and duration of toxic episodes rather than increased mean ANC levels (Baker et al. 1982). In the 1980s, Lake Langtjern experienced long periods of low pH, low ANC and high Al₃ (Fig. 3). Episodes of pH < 4.8 decreased considerably both in duration and frequency since the peak in 1989, but periods of pH < 4.8 still occur, e.g. a possible 15-day period in 2012. If these periods cause mortality in the youngest individuals or the fertilized eggs in the stream substrate, the population would still have irregular setbacks in producing offspring. Serrano et al. (2008) proposed that pH, not Al, is most important for trout survival in organic-rich boreal streams. Juvenile brown trout mortality in such streams was modelled with 80 % mortality during 14 days of pH 4.8. The Lake Langtjern outlet had episodes in 2007 and 2009 where pH possibly was below 4.8 for 63 and 35 days, respectively. These episodes may have inflicted high mortality in several year-classes of brown trout, even though the yearly means for pH were 5.0 and 5.1, respectively. Longer episodes of Al₃ > 50 µg l⁻¹ have been few
since 1997, but week-long episodes probably occurred in both 2006 and 2007. Such episodes may have caused high mortality in young-of-the-year brown trout.

In addition to the water chemistry, habitat characteristics probably limit the brown trout population in Lake Langtjern. Suitable spawning areas are few and the number of spawning fish is low, as the remaining individuals from the stocking in 2006 and 2003 probably only exist in small numbers. The inlet stream (LAE02) has more suitable substrate, but it is also a smaller stream than the outlet. Both streams are subject to winter and summer droughts. Our catches document that successful spawning is occurring. The number of spawners has been higher before, without resulting in successful reproductions. The present reproduction therefore indicates that the change in water chemistry is the crucial factor.

Funding: Monitoring of water chemistry in Lake Langtjern is funded by the Norwegian Environment Agency and, since 2013, also by the Ministry of Climate and Environment through a grant supporting continuation of long time series. This work was funded in part by the Norwegian Research Council project “Lakes in Transition” (244558/E50) and the Norwegian Institute for Water Research (NIVA).

Conflict of Interest: The authors declare that they have no conflict of interest.

References


Table 1 Lake Langtjern outlet water chemistry mean values ± SD in five periods from 1973 to 2014. No data for 1984–1985. Data for Al, TOC and ANC from 1986

<table>
<thead>
<tr>
<th>Period</th>
<th>SO$_4$</th>
<th>NO$_3$</th>
<th>pH</th>
<th>Al$_i$</th>
<th>ANC</th>
<th>ANC$_{oaa}$</th>
<th>TOC</th>
<th>Ca</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>µeq l$^{-1}$</td>
<td>µeq l$^{-1}$</td>
<td>µg l$^{-1}$</td>
<td>µeq l$^{-1}$</td>
<td>µeq l$^{-1}$</td>
<td>mg C l$^{-1}$</td>
<td>µeq l$^{-1}$</td>
<td></td>
</tr>
<tr>
<td>1973–1979</td>
<td>72 ± 14</td>
<td>1.9 ± 1.3</td>
<td>4.9 ± 0.2</td>
<td>27 ± 11</td>
<td>69 ± 12</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1980–1989</td>
<td>66 ± 14</td>
<td>1.7 ± 1.3</td>
<td>4.8 ± 0.2</td>
<td>74 ± 19</td>
<td>13 ± 8</td>
<td>-15.3 ± 8.8</td>
<td>8.8 ± 1.6</td>
<td>57 ± 11</td>
</tr>
<tr>
<td>1990–1999</td>
<td>51 ± 14</td>
<td>1.5 ± 1.2</td>
<td>5.0 ± 0.2</td>
<td>46 ± 20</td>
<td>32 ± 12</td>
<td>-2.3 ± 9.1</td>
<td>10.1 ± 2.0</td>
<td>55 ± 10</td>
</tr>
<tr>
<td>2000–2007</td>
<td>25 ± 6</td>
<td>0.9 ± 0.7</td>
<td>5.1 ± 0.2</td>
<td>27 ± 9</td>
<td>47 ± 12</td>
<td>10.6 ± 8.7</td>
<td>10.8 ± 1.9</td>
<td>47 ± 10</td>
</tr>
<tr>
<td>2008–2014</td>
<td>17 ± 4</td>
<td>0.8 ± 0.7</td>
<td>5.1 ± 0.2</td>
<td>26 ± 7</td>
<td>47 ± 9</td>
<td>9.7 ± 6.9</td>
<td>11.0 ± 2.0</td>
<td>42 ± 8</td>
</tr>
</tbody>
</table>
Table 2 Number of non-stocked fish caught by electrofishing in the outlet and major inlet to Lake Langtjern in the period 2010–2014. No data for inlet 1014.

<table>
<thead>
<tr>
<th>Age class</th>
<th>Year</th>
<th>2010</th>
<th>2011</th>
<th>2012</th>
<th>2013</th>
<th>2014</th>
</tr>
</thead>
<tbody>
<tr>
<td>Outlet</td>
<td>0+</td>
<td>0</td>
<td>2</td>
<td>13</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>&gt;0+</td>
<td>6</td>
<td>5</td>
<td>1</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Inlet</td>
<td>0+</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>n.a.</td>
</tr>
<tr>
<td></td>
<td>&gt;0+</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>n.a.</td>
</tr>
</tbody>
</table>
Fig. 1 Map showing the position and the catchment (dotted line) of Lake Langtjern (60.37 N, 9.73 E), a research station for studying acidification of surface waters in Norway. Outlet (LAE01) and inlets (LAE03, LAE02 and LAE08) are indicated.

Fig. 2 Annual deposition of SO$_4$, and yearly mean concentrations of SO$_4$, Ca, ANC, ANCoaa, pH and Al in the outlet at Langtjern over the period 1973–2014. Deposition data from Aas et al. (2016)). No outlet data for 1984–1985. TOC and Al analysed from 1986. Dotted lines indicate levels of significant changes in the data series.

Fig. 3 Count of consecutive days of pH < 4.8, ANC < 10 µeq l$^{-1}$, ANCoaa < -5 µeq l$^{-1}$ and Al > 50 µg l$^{-1}$ at the outlet of Lake Langtjern 1973–2014. No data for 1984–1985, and data for ANCoaa and Al from 1986.

Fig. 4 Number of stocked (top) and captured (bottom) brown trout (n/100 m$^2$) in Lake Langtjern in the period 1972–2011.