

The survival of a small isolated brown trout population (*Salmo trutta*) in a harsh environment in the remote Lysedalen, Rogaland

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Sammendrag

Overlevelse av en liten isolert aurebestand under marginale miljøforhold øverst i Lysedalen: Mange høyereliggende innsjøer på Sør-Vestlandet har aldri hatt fiskebestander, enten på grunn av marginale miljøforhold, eller fordi det aldri har vært satt ut fisk. De aurebestandene som i utgangspunktet fantes i disse marginale områdene, døde stort sett ut som følge av forsuring i 1960- og 1970-årene. En liten isolert bestand øverst i Lysedalen er imidlertid et unntak. Overraskende nok har denne bestanden overlevd i årevis under helt marginale forhold. Fisken var imidlertid i dårlig forfatning, trolig på grunn av et liv helt på eksistensminimum, i tillegg til mulige effekter av innavl. Det ligger en liten esker ("slukås") rett øst for Langetjørn, og bekken som

drenerer eskerområdet hadde en median kalsiumkonsentrasjon på 0,83 mg/l, mot 0,19 mg/l i de andre bekkene. Det noe høyere Ca-innholdet skyldtes trolig innslag av lettere forvitrelige mineraler i eskeren. På grunn av de vannkjemiske effektene av denne geologiske "tilfeldigheten" overlevde auren i Langetjørn forsuringen, mens de andre bestandene i området døde ut. Som følge av redusert forsuring har Langetjørnbestanden nå rekolonisert flere av de andre små tjernene på toppen av Lysedalen.

Summary

Many high mountain lakes in southwestern Norway have never supported trout populations, due to lack of initial stockings and/or marginal environmental

conditions. The trout populations originally found in these mountain areas largely became extinct in the 1960s and 1970s due to acidification. An isolated brown trout population in Langetjørn in Lysedal represents a rare exception. This population has, against all odds, apparently survived both the acidification and the extremely harsh environmental conditions in Lysedal. The population health was however poor, probably due to adverse effects of living in marginal environmental conditions, and possible effects of inbreeding. A small esker is located east of Langetjørn. In Stjernebekken, the tiny brook draining the esker area, median calcium concentration was determined to 0.83 mg/l, as opposed to 0.19 mg/l in the remaining brook samples. The elevated Ca-level in Stjernebekken was probably caused by presence of somewhat easier weatherable minerals within the esker. The water chemical effect of this extremely local geological "coincidence" apparently saved the trout population in Langetjørn from extinction due to acidification, while those in the remaining lakes became extinct. Due to the recovery of the water chemistry recent years, the Langetjørn population has recolonized the other small lakes and river stretches at the top of Lysedal.

Introduction

The general perception has been that brown trout (*Salmo trutta*) originally was found in most of the lakes in Norway (Huitfeldt-Kaas 1924). However, recent research has established that many lakes,

primarily remote high mountain lakes in western Norway, never have supported trout populations. In Rogaland County these lakes make up 13% of the registered lakes (Hesthagen et al. 1997). In the Lyse area, this category of lakes is highly overrepresented and only a minor fraction of the lakes in these mountains has supported trout populations (Sevaldrud and Muniz 1980). A recent study has suggested ion deficit as an important restrictor to trout population in these extremely dilute water qualities (Enge and Kroglund 2010).

From the eastern part of the remote valley Lysedal in Rogaland, only a population in the valley bottom was known. Due to steep river stretches and the lack of immigration possibilities from downstream, the trout population in the small lakes at the top of Lysedal appears as one isolated population.

Some remote trout populations in southern Norway experienced population reductions and possible extinction as early as the 1850s (Dahl 1921, Huitfeldt-Kaas 1922). Qvenild et al. (2007) suggested that these population effects might have been the first early signs of acidification. During the 1960s and 1970s, nearly all trout populations in the mountain lakes and a large fraction of those located at lower altitudes, were wiped out due to acidification (Hesthagen et al. 1997, Jensen and Snekvik 1972, Sevaldrud and Muniz 1980).

During the last decades, however, both water chemical and biological recovery have been observed throughout southwestern Norway (Hesthagen and

Forseth 1998, Hesthagen et al. 2001, Hesthagen et al. 2011, Raddum et al. 2001). In the neighbouring river to Lyseelv, Sira, acidification is no longer considered as a limiting factor for the trout populations (Enge and Hemmingsen 2010).

Due to the remoteness of Lysedalén, only limited data concerning fish and water chemistry has been collected during the years. Unfortunately, no data exists from the acidification period, but considering the severe acidification damages in adjacent areas, and the marginal environmental conditions in Lysedalén, the trout population was assumed extinct. However, in the autumn 2008, an unexpected observation of trout in the

river upstream Raudbergjørn was made (T.E. Børresen, pers.comm.). The aim of the present study was to establish if this observation represented a dying population, or actually a sustainable population.

Study area

Lysefjorden, and the eastern extension, Lysedalén, appears as a spectacular “ax cut” in a large barren bedrock plateau. Along the fjord the altitude of the plateau is about 600-700 m, and the fjord is 450 m deep. Lysedalén is a steep, narrow V-shaped valley, starting at the inner end of the fjord (Lysebotn) and rising up to about 850 m in the east. In the valley bottom sparse moraine and glacial deposits were found, and between Stjernetjørn



Lysefjorden appears as a spectacular “ax cut” in a large barren bedrock plateau. Along Lysefjorden the altitude of the plateau is about 600-700 m, and the fjord is 450 m deep (Photo: Audun Steinnes).

Lake	Altitude m	Area km ²	Max depth m
Raudbergjørn	790	0.024	7
Austre Langetjørn	805	0.008	5
Vestre Langetjørn	805	0.004	2
Rundetjørn	810	0.008	7
Krokevatn	850	0.012	2

Table 1. Lakes included in the study.

and Austre Langetjørn a small esker (30x60m) is located. The forest limit in Lysedalen is located about 600-700 m above sea level. The altitude of the eastern part of the plateau, along Lysedalen, is about 1000-1100 m. The plateau bedrock is exceptionally poor, and consists of slowly weatherable rock types, primarily gneisses and granite. Glacial deposits are virtually absent, and the vegetation is sparse.

Due to the geology and the altitude, the water quality in the lakes in these mountain areas is extremely dilute. Calcium as low as 0.05 mg/l was recently measured in lakes somewhat north of the study area (Enge 2011).

The study area, Figure 1, is located at the top of Lysedalen, at an altitude of about 800 m, and includes the small lakes Raudbergjørn, Austre Langetjørn, Vestre Langetjørn, Rundetjørn and Krokevatn, Table 1. Austre and Vestre Langetjørn are connected by a short strait, and are in fact the same lake. Due to short distances and excellent migration possibilities between most of the lakes and the river stretches, the trout in the area was considered as one population.

During water sampling, maximum depths of the lakes were measured to

2-7 m, Table 1. With an ice cover of 1-2 m during winter, the available volume to fish is highly restricted, and the water temperature is close to the freezing point.

Water from the barren plateaus, on both sides of the valley, drains down into Lysedalen to Lyseelv. On the top of Lysedalen the river is actually a small brook. The average annual water flow is 0.03 m³/sec upstream the tributary from Langetjørn. This part of the river includes a lot of small ponds, being up to 100 m long, 10-20 m width and 1-2 m deep. This enables presence of a stationary population of trout in the brook, despite the size. At the outlet of Raudbergjørn, the water flow has increased to 0.18 m³/sec.

The specific runoff in this part of Lysedalen is about 80 l/s per km² (NVE.no 2012), representing a precipitation of 2500-3000 mm. The precipitation may fall as snow as early as October. Thin ice cover may occur sporadically as early as September, but the persistent ice cover usually do not occur until November or December. The snowmelt usually takes place in May, and the ice cover normally disintegrates during early June.

At Auråhorten, about 10 km further to the north on this mountain plateau,

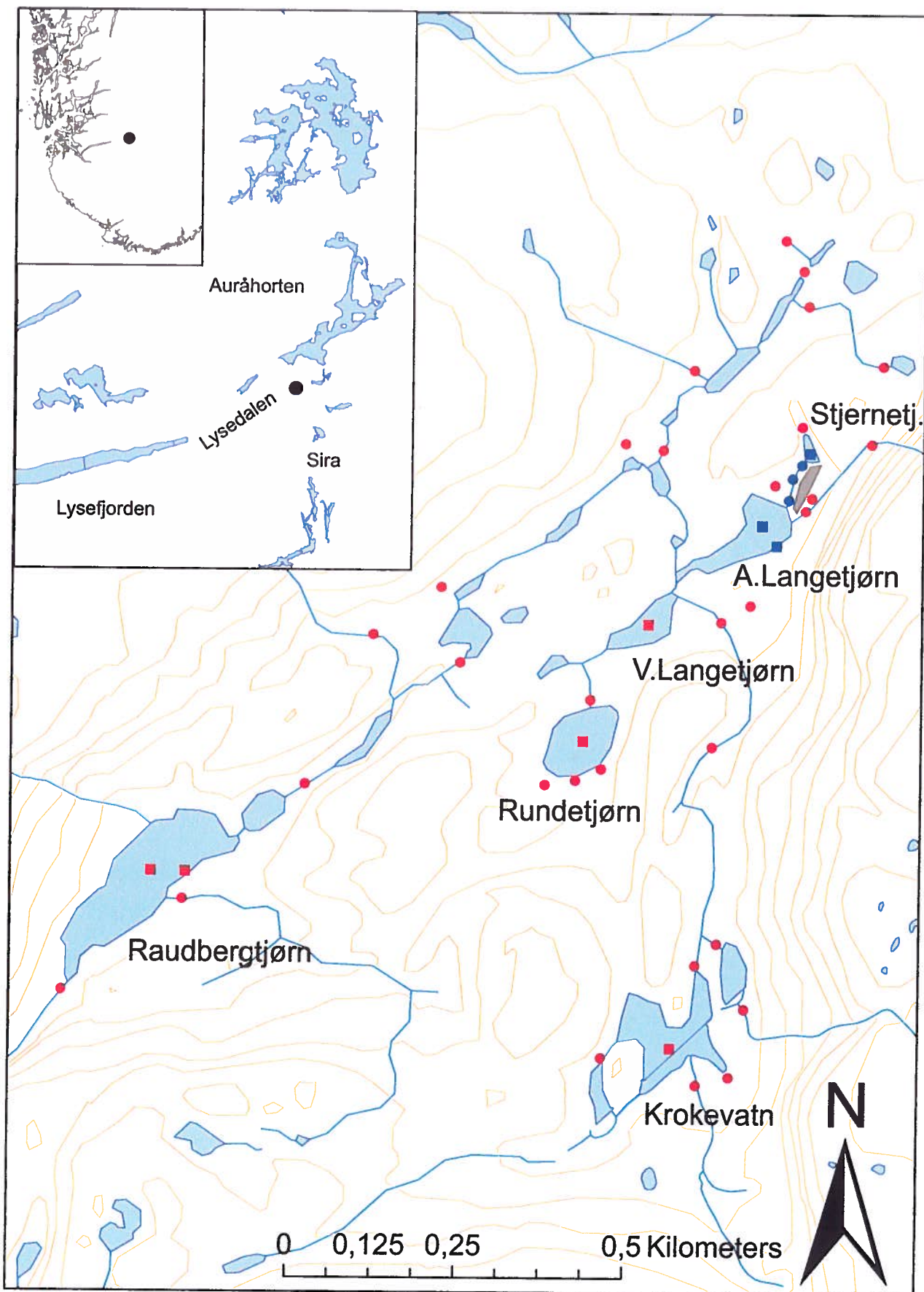


Figure 1. Map, showing the test fished lakes and the water sampling locations. (Squares: Lakes samples; Circles: Brooks and inlets/outlets of lakes; Gray: Esker; Blue: Water quality affected by the esker; Red: No (or limited) water chemical effect of the esker).



Raudbergstjørn, the largest lake in Lysedalen. Spawning is restricted by a water fall and a very rocky substrate (Photo: Espen Enge).

the average snow accumulation during winter is 1420 mm water equivalents (Sira-Kvina Power Company, unpublished data). With a density at late winter of 43%, this represents in average 3.3 m of snow. More than 5 m of snow has earlier been registered at Auråhorten (Sira-Kvina Power Company, unpublished data).

In the 1970s, fish status in 17 lakes in the Lyse watershed was registered (Sevaldrud and Muniz 1980). Fourteen of the lakes had never supported trout, two lakes had sparse populations, and one lake had a dense trout population. All lakes with fish populations were located in the western part of the watershed. None of the lakes at the mountain plateaus on

both sides of Lysedalen have ever supported trout populations. Possible explanations to the general absence of trout populations in the eastern area, may be lack of initial stockings, or marginal environmental conditions.

Methods

Water chemistry

Sampling was performed during the period May 2009 to June 2011. Water was sampled from brooks, lake inlet/outlets and at several depths of the lakes. Normally the depths 0-1 m, 2-3 m and 4-5 m were used, depending on maximum depth of the current lake, eventually ice cover and ice thickness. Samples were

collected in new 200 ml PE-bottles, stored cool, and analyzed for pH, conductivity, alkalinity, Al and color within 48 hours. The other parameters were analyzed within 2 weeks.

pH was measured with a Orion pH-meter with Radiometer electrode pHC2401, calibrated with standard buffers (pH=4.01&6.86). Conductivity was measured with conductivity meter Cyberscan PC300 calibrated with standard KCl-solutions (reference temperature = 25 °C). As other studies of fish and water quality (Enge and Kroglund 2010, Sevaldrud and Muniz 1980), the current study consequently uses H⁺ adjusted conductivity (1 µeq/l H⁺ = 0.35 µS/cm). Alkalinity was titrated to fixed endpoint pH=4.50 with sulfuric acid, and "equivalence alkalinity" (ALKe) was calculated according to Henriksen (1982). Color was determined photometrically at 410 nm in 50 mm glass cuvettes, and measured on unfiltered samples due to negligible turbidity. Ca, Na and Cl were measured potentiometrically with Radiometer ion selective electrodes, equipped with an external calomel reference electrode. Magnesium was determined photometrically with calmagite, after selectively complexing Ca with EGTA (Hach 2003). None-marine Mg (notation: Mg*), was calculated by subtracting the marine Mg contribution, estimated from chloride, from the measured Mg (Skartveit 1980). Total monomeric aluminium was determined photometrically with Eriochrome Cyanine R (Eaton et al. 1995). This method is an alternative to the more commonly used pyrocatechol-method.

Fish

Test fishing was performed in the autumn of 2009 and in the spring of 2010, with multimesh nets. "SNSF"-nets (Rosse-land et al. 1979) were used in Langetjørn and Raudbergtjørn, while "Nordic" nets (Appelberg et al. 1995) were used in Krokevatn. The first type of nets includes mesh sizes in the range of 10-45 mm, and the latter 5-55 mm. These two types of nets have, however, about equal efficiency in catching brown trout (Jensen and Hesthagen 1996, Appelberg et al. 1995).

A serious problem concerning the effort arises when examining small populations. Even limited test fishing may take out a large fraction of the population. The effort used was 1-2 nets in each lake. Apparently this is a low effort. However, considering the limited area of the lakes, this effort is rather large. Five nets in four lakes of a total lake area of 0.048 km² equal 104 nets per km².

CPUE (Catch Per Unit Effort) was calculated as number of fish per 100 m² net area per night of fishing.

On each fish, length (to the nearest 0.5 cm), weight (to the nearest 1.0 g), sex, maturity, flesh coloration and diet (content of stomach) were determined. Age determination was performed on scales.

The condition factor (CF) was calculated by Fultons formula (Nash et al. 2006).

Results

Water chemistry

In total 83 samples were analyzed from different localities in Lysedalen. The

samples were divided into two selections, lake samples from 2-3 depths, Table 2, and brooks samples, Table 3. The latter also includes inlets and outlet brooks from the lakes.

In general, the water quality was slightly acidic (pH=5.13-6.30, median =5.59, n=83), and the conductivity was extremely low (3.8-25.4 $\mu\text{S/cm}$, median

=7.1 $\mu\text{S/cm}$, n=83). The Ca values were also very low (0.08-3.2 mg/l, median =0.29 mg/l, n=83), suggesting limited resistance to acidification.

Due to the shallowness of the lakes, only limited water chemical depth gradients were found. Standard deviations of pH-values at several depths from Austre Langetjørn were 0.01-0.04 at the five

Lake	Date	Temp. °C	pH	Cond. $\mu\text{S/cm}$	ALKe $\mu\text{eq/l}$	Ca mg/l	Mg mg/l	Na mg/l	Color mg Pt/l	Al $\mu\text{g/l}$	Cl mg/l
Krokevatn*	04-Jun-11	5.0	5.33	6.5	5	0.15	0.13	0.78	5	-	1.2
A.Langetjørn*	22-May-10	5.0	5.59	9.6	30	0.61	-	0.87	5	32	1.3
A.Langetjørn	10-Oct-10	6.5	5.81	7.3	19	0.36	0.09	0.70	10	-	0.8
A.Langetjørn	21-Dec-10	0.5	5.74	9.7	27	0.58	0.13	0.99	10	-	1.2
A.Langetjørn	09-Mar-11	-	5.61	10.7	34	0.61	0.12	0.86	5	-	1.1
A.Langetjørn	04-Jun-11	2.0	5.61	9.6	20	0.42	0.13	0.94	4	-	1.6
V.Langetjørn*	22-May-10	5.0	5.59	7.1	19	0.40	-	0.70	7	29	1.1
V.Langetjørn*	04-Jun-11	7.5	5.55	8.3	12	0.28	0.13	0.92	6	-	1.5
Rundetjørn	10-Oct-10	6.5	5.69	6.1	13	0.23	0.08	0.67	13	-	0.7
Rundetjørn	21-Dec-10	0.5	5.60	8.3	16	0.33	0.12	0.96	13	-	1.1
Rundetjørn	04-Jun-11	5.5	5.46	9.4	14	0.29	0.15	1.1	6	-	1.8
Raudbergtjørn*	07-Sep-09	-	5.63	6.4	8	0.25	-	0.70	11	31	1.3
Raudbergtjørn	22-May-10	5.8	5.36	7.3	14	0.20	-	0.86	8	42	1.3
Raudbergtjørn	04-Jun-11	6.0	5.36	6.5	2	0.17	0.13	0.75	5	-	1.2

Table 2. Median values of lake samples from 3 (2*) depths (conductivity: H⁺-adjusted).

Brook	Period	n	pH	Cond. $\mu\text{S/cm}$	ALKe $\mu\text{eq/l}$	Ca mg/l	Mg mg/l	Na mg/l	Color mg Pt/l	Al $\mu\text{g/l}$	Cl mg/l
Stjernebekken	2010-2011	8	6.14	9.2	46	0.83	0.11	0.70	13	-	1.1
(all other brooks)	2009-2010	38	5.53	6.2	9	0.19	0.07	0.72	8	32	0.9

Table 3. Median values of all brook, inlet and outlet samples (conductivity: H⁺-adjusted). Detailed results from all the individual samples are presented in Enge (2010) and Bredal and Vatsvåg (2011).

sampling dates. The corresponding Ca standard deviations were 0.00-0.19 mg/l.

Stjernebekken, Table 3, also includes three samples from 0-2 m in Stjerne-tjørn, a little pond in the brook. Stjernebekken had considerably better water quality than the rest of the localities. Alkalinity and calcium were 4-5 times higher than the other brooks, and median pH was 6.14, Table 3.

The conductivity in the current lakes and brooks correlated both to Na ($r^2=0.60$, $p<0.001$, $n=81$), and Ca ($r^2=0.58$, $p<0.001$, $n=81$). In a multiple regression, these two parameters explained nearly the entire variation in conductivity ($r^2=0.98$, $p<0.001$, $n=81$).

When excluding the localities strongest affected by the esker (Stjernebekken and Austre Langetjørn), the conductivity of the remaining localities was acceptable explained by Na alone ($r^2=0.83$, $p<0.001$, $n=53$). Ca alone was less correlated to conductivity in this selection of samples ($r^2=0.39$, $p<0.001$, $n=53$).

Non-marine magnesium (Mg^*) was estimated to 0.04 ± 0.03 mg/l ($n=54$), or without the localities affected by the esker 0.03 ± 0.02 mg/l ($n=36$). The esker affected localities had $Mg^*=0.05\pm 0.04$ mg/l ($n=18$).

Fish

In total 14 trout were caught at an effort of 5 nets, Table 4. The calculated CPUE values (Catch Per Unit Effort) were 15 ind./100 m² per night of fishing (Raudbergstjørn) and 7 ind./100 m² (Langetjørn). According to EU Water Framework Directive Classification (Iversen 2009), these CPUE-values represent “moderate” and “low” population densities.

The net catch was dominated of rather small trout, Table 4 and Figure 2. The condition factor was very low, about 0.8, and decreased with increasing body length ($r^2=0.48$, $p<0.01$, $n=14$). The age was determined to 2+ to 6+ on scales, Figure 2. However, body shape, head shape and external coloration suggested that the older trout might have been considerably older. Nine of the 14 trout were spawners, of which 7 were formerly spawners. In the oldest females from Langetjørn, several generations of residual roe had merged into a gray jelly-like substance. Some trout from Langetjørn were probably blind, or close to blindness (cloudy lens), and one fish had protruding eyes. The majority of the trout had scales with resorbed edges, Table 5. The growth rate first years was about

Lake	Date	Nets		Trout #	Weight (g)		Condition factor	
		#	type		Average	SD	Average	SD
Raudbergstjørn	Sep-09	1	SNSF	6	110	52	0.81	0.11
Krokevatn	Sep-09	1	Nordic	0	-	-	-	-
A.Langetjørn	Sep-09	1	SNSF	0	-	-	-	-
A.+V.Langetjørn	May-10	2	SNSF	8	60	18	0.80	0.06

Table 4. Results of test fishing in lakes in Lysedalen.

normal for this part of Norway (5 cm/yr), but stagnation occurred at age 4-5 yr. Asymptotic length(∞) was estimated to 23 cm (Langetjørn) and 32 cm (Raudbergjørn). Combination of length(∞) and the corresponding condition factors ($CF_{L\infty}=0.74$ & 0.66) yields weight(∞) = 90 g (Langetjørn) and 216 g (Raud-

bergjørn). This is fairly close to the largest trout caught in these two lakes during the current test fishing. Twelve of 14 trout had white flesh coloration, and the remaining two specimens; light red. The registered diet was water insects exclusively.

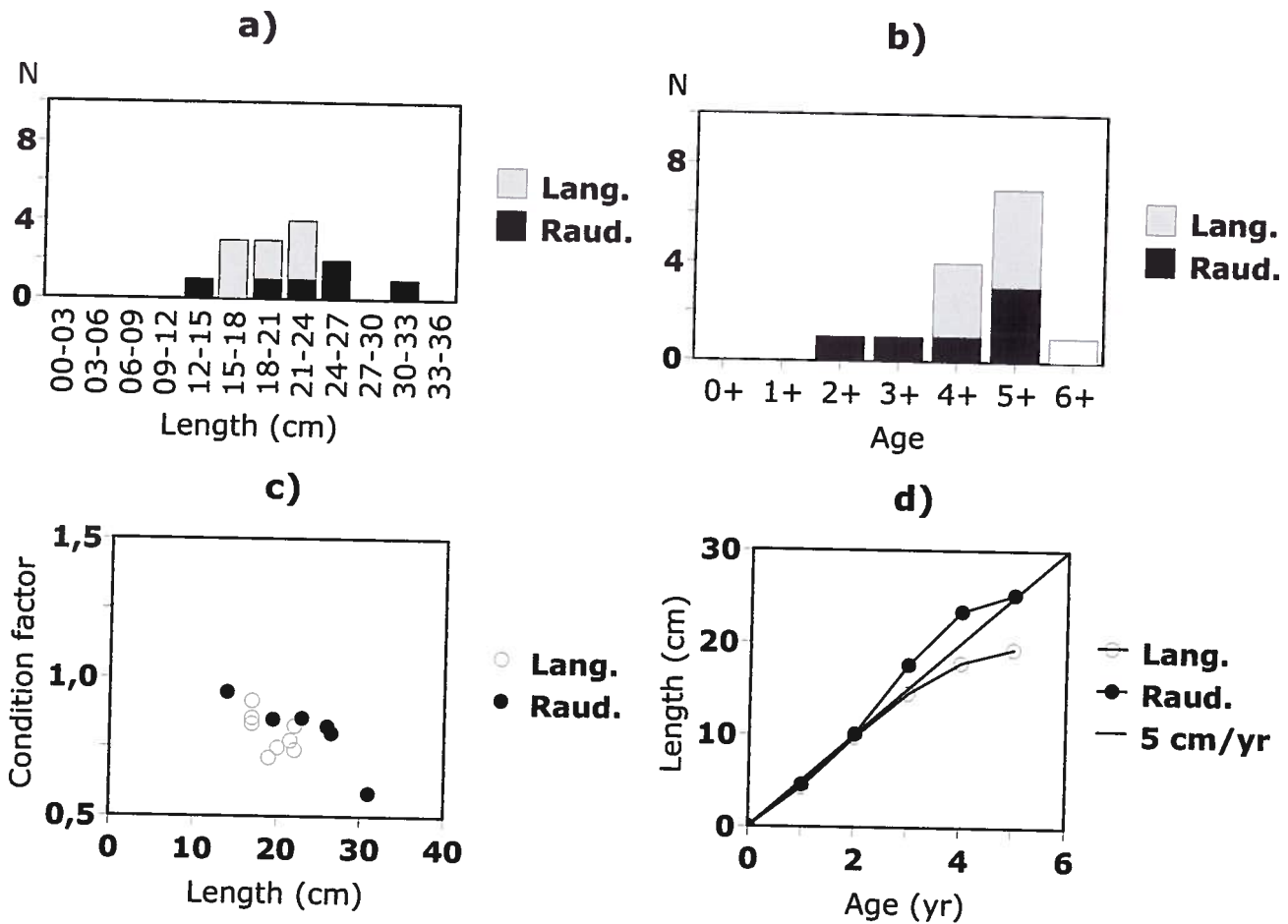


Figure 2. Test fishing results from Raudbergjørn and Langetjørn. a) length distribution, b) age distribution, c) condition factor and body length and d) growth.

Lake	n	Scale resorption		
		none	limited	extensive
Raudbergjørn	6	1	4	1
Langetjørn	8	3	2	3

Table 5. Scale resorption, trout from Raudbergjørn and Langetjørn.



Trout at spawning area in a stagnant pool in the inlet to Rundetjørn (Photo: Espen Enge).

Of other localities, trout was observed in Rundetjørn (inlet) and at the entire river stretch upstream Raudbergtjørn. The single trout observed in Rundetjørn was probably blind too (cloudy lens). No fish was caught in Krokevatn.

Discussion

The little esker between Stjernetjørn and Austre Langetjørn had a distinct, but primarily local effect on the water chemistry. At sampling in October 2010, calcium in Stjernebekken increased from 0.37 mg/l at the inlet to Stjernetjørn, to 0.75 mg/l at the outlet (Bredal and Vatsvåg 2011). Stjernetjørn is a shallow pond in Stjernebekken, dammed by the esker. At the 60 m brook stretch from Stjernetjørn, along the esker, and down

to Austre Langetjørn Ca in Stjernebekken increased from 0.75 mg/l to 0.96 mg/l, suggesting a Ca value of about 3 mg/l in the water leaking from the esker. Considerably larger glacial deposits than the esker were found at other locations within the area, but without having any effect on the Ca-values. Thus, the water chemical effect of the esker was most likely caused by presence of somewhat easier weatherable minerals within this particular esker, probably due to glacial drift. Far travelled glacial material from as far east as Oslofjord and Baltic region has earlier been found in Rogaland (Andersen et al. 1987). The water chemical effect of the esker was also apparent in Austre Langetjørn (median Ca=0.36-0.61 mg/l). Vestre Langetjørn, however,

had Ca-values not significantly different from that in other localities in the area.

Due to the generally slow weathering bedrock minerals, the marine ion contribution, expressed as chloride, normally determines the conductivity in waters in this mountain area (Enge 2009, Enge and Kroglund 2010). The conductivity in the study lakes and brooks, however, was determined both by the marine influence, represented by Na, and the geology, represented by Ca. In total, these two variables counted for nearly the entire conductivity. However, when excluding the localities strongest affected by the esker (Stjernebekken and Austre Langetjørn), the conductivity of the remaining localities was acceptable explained by the marine ion contribution alone, represented by Na. This is in accordance to the general water chemical pattern from these mountain areas (referred earlier).

Generally, low levels, and only small differences in Mg^* between the sample selections were found, suggesting that

the water quality enrichment effect of the esker, primarily was caused by Ca-minerals, and not by Mg.

With an average water flow of 1.3 l/sec, Stjernebekken is probably not large enough for spawning. However, the Lysedal trout strain is a possible lake spawner. Spawning areas was observed in a stagnant pool in the main inlet to Rundetjørn 10-Oct-2010, and at several locations along the shoreline of Rundetjørn. Lake spawning in Austre Lange-tjørn, having better water quality than Rundetjørn, is highly expected.

In extremely dilute water, having conductivity $<14 \mu S/cm$, the population density of brown trout is primarily determined by conductivity and pH alone (Enge and Kroglund 2010). When plotting the median pH and conductivity from lake samples into the Enge-Kroglund diagram, Figure 3, the lakes above the curved line ("pH critical") normally have moderate to dense trout populations, and the lakes below the line are

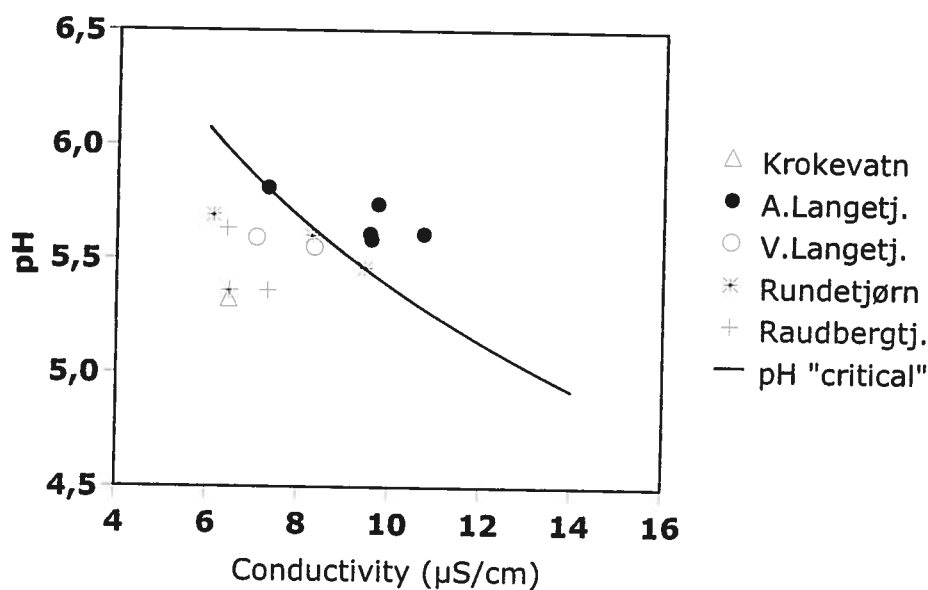


Figure 3. Plot of median lake water chemistry. The curved line ("pH-critical") is referred to Enge and Kroglund (2010).

either extinct or close to extinction. Sparse populations normally appear close to the line, approximately ± 0.1 pH.

The applicability of the model to the current lakes seemed adequate. According to the diagram, Figure 3, the population density of trout was expected to be moderate in Austre Langetjørn, sparse in Vestre Langetjørn and extinct in Krokevatn. This was basically in accordance to the test fishing results.

Raudbergtjørn, however, represented a considerable deviation. The test fishing yield suggested a moderate population density, while the model indicated an extinct population. The explanation to this discrepancy is probably that the trout population in Raudbergtjørn is recruited by immigration from upstream lakes and river stretches, and not by local reproduction. Spawning in the inlet river is restricted by a waterfall, and a very rocky substrate at the short stretch downstream from the waterfall to Raudbergtjørn. Thus, the water quality in Raudbergtjørn is not representative for the recruitment to the lake.

Due to lack of data, a crucial question is the status of the trout populations during the acidification period. In Austre Langetjørn the sum of non marine base cations, normally considered equal to the original alkalinity, was estimated to 36 $\mu\text{eq/l}$ (2009-2011 data). Based on 1986-data from 3 larger neighbouring lakes, included in the "1000 lakes survey" (Lien et al. 1987), the acidification (loss of alkalinity) was estimated to 31 ± 3 $\mu\text{eq/l}$. Assuming this acidification was representative to the current lakes, and

no change in base cation concentration during the period has taken place the 1986-alkalinity in Austre Langetjørn was estimated to 5 $\mu\text{eq/l}$. Regarding the latter assumption, a large regional water chemical survey in Rogaland did not reveal any changes in Ca from 1987 to 2002 ($p > 0.01$), despite the decreasing acidification (Enge and Lura 2003). Based on a multiple logarithmic regression of pH against ALKe and color from the current lake samples ($r^2 = 0.65$, $p < 0.001$, $n = 36$), the corresponding pH to the 1986-alkalinity was estimated to 5.45, representing an estimate of the minimum pH during acidification. This pH was slightly below the estimated critical pH at the current conductivity, Figure 3, suggesting that the trout population in Austre Langetjørn barely survived the acidification. Austre Langetjørn had definitely the best water quality of the current lakes. Thus, the inevitable conclusion is that the populations in the other lakes did not survive the acidification period. The trout found in these lakes today is probably immigrants from Austre Langetjørn, or offspring from immigrants.

The recruitment to lakes, apparently having detrimental water quality, may still be sufficient, if brooks with acceptable water quality are available for spawning (Hesthagen and Jonnson 1998). However, a comprehensive water chemical survey did not discover such localities in the project area except for Stjernebekken in Austre Langetjørn, as previously discussed.

Borgstrøm (1992) presented population estimates for trout from four Nor-

wegian mountain lakes, having densities from about 10 to 200 specimens/ha. Applying 50 trout/ha as a very rough estimate, the total population in the Lysedal lakes counts only about 250 trout, or 20-120 specimens in the individual lakes. Regardless of the representativeness of the applied density, this anyhow establishes that the population is very small.

The current study included only 14 trout. However, the registered biological parameters showed relatively small variations, both within and between the lakes, suggesting a reasonable representativeness of the obtained test fishing data.

The general health of the trout caught in Lysedalen was poor. Even though many factors may cause adverse health effects, we cannot reject the possibility of the observed effects, being caused by marginal environmental conditions, both physical and with respect to water chemistry.

Enge and Kroglund (2010) suggested that conductivity $<5 \mu\text{S}/\text{cm}$ is detrimental to trout, at least to early life stages. Further, Wathne and Rosseland (2000) suggested that $0.38 \text{ mg}/\text{l}$ of Ca is required to sustain healthy populations of trout in mountain lakes. Even in Austre Langetjørn, the only lake meeting these requirements, the main inlet was periodically far more dilute ($\text{Ca}=0.08 \text{ mg}/\text{l}$ and $\text{Cond}=4.6 \mu\text{S}/\text{cm}$ in October 2010). Due to short retention time (Langetjørn: 3 days at average water flow), such dilute water may dominate the water quality in the lake completely during high flow situations, regardless of the small Ca-leakage from the esker.

The trout caught in the study lakes was relatively old, as 12 of 14 specimens had an age of 4+ or older. However, external morphological features suggested that some of the trout might have been older. Age determination on scales systematically underestimates the age of older trout ($>4 \text{ yr}$), especially at slow growth (Hesthagen 1985). The presence of stagnation edge on some of the scales supported this assumption. This suggests an accumulation of old fish in the population due to apparently limited recruitment.

Additional to possible lake spawning, the trout in Langetjørn has excellent spawning areas in the main inlet brook, coming from Krokevatn. Despite several site visits throughout the study period, no trout was ever observed. Apparently this brook was avoided by the trout, possibly due to inconvenient dilute water.

Several of the observed adverse health effects may also be associated with inbreeding. Due to the "bottleneck" effects of small population size and limited reproduction (Prodöhl et al. 1997), effects of inbreeding cannot be rejected. The detrimental effects of inbreeding are especially apparent in harsh environments (Miller 1994, Crnokrak and Roff 1999).

Conclusion

The current study concludes that the water quality in Austre Langetjørn was acceptable to trout even during the severe acidification in the 1980s, and subsequently that the original trout population has survived. The population is currently sustainable, and has recolonized the other lakes at the top of Lysedalen.

The study also suggests that the poor population health was caused by direct or indirect effects of the harsh environmental conditions in Lysedalén.

Acknowledgments

The authors thank Sindre Ditolvsen, Espen B. Jacobsen, Fredrik Berg-Larsen, Ole Tobias Lima and Mathias Nilsen for excellent field and laboratory assistance, and Trond Erik Børresen for making the map. We also thank Dr. Trygve Hesthagen for valuable comments to the manuscript and Michael S. Nilan for checking the language. The survey was financially supported by County Governor of Rogaland.

References

- Andersen, B.G., Wangen, O.P and Østmo, S.R. 1987: Quaternary geology of Jæren and adjacent areas, southwestern Norway. *Norges Geologiske undersøkelse, Trondheim. Bulletin 411: 1-55*
- Appelberg, M., Berger, H.M., Hesthagen, T., Kleiven, E., Kurkilahti, M., Raitaniemi, J. and Rask, M. 1995: Development and intercalibration of methods in Nordic freshwater and fish monitoring. *Water, Air and Soil Pollution 85: 401-406*
- Borgstrøm, R. 1992: Effect of population density on gillnet catch ability in four allopatric populations of brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences 49:1539-1545*
- Bredal, M. and Vatsvåg, H. 2011: Vannkjemiske undersøkelser i Lysevassdraget 2010-11. *BSc-thesis, University of Stavanger*. In Norwegian. Water chemical surveys in Lyse 2010-11.
- Crnokrak, P. and Roff, D. 1999: Inbreeding depression in the wild. *Heredity 83: 260-270*
- Dahl, K. 1921: Undersøkelser over ørretens utdøen i det sydvestligste Norges fjeldvand. *Norges Jæger og Fiskerforenings Tidsskrift 50: 249-267*. In Norwegian. Extinction of brown trout in mountain lakes in southwestern Norway. (Norwegian Hunter and Anglers Society's Journal)
- Eaton, A. D., Clesceri, L. S., Greenberg, A. E. (Eds) 1995: Standard methods for the examination of water and wastewater (19.edt.). *American public health association, American water works association & water environment federation, Washington DC*
- Enge, E. 2009: Sira-Kvina utbyggingen - Effekter på vannkjemi, forsureingssituasjon og fiskebestander i Sira. *MSc-thesis, University of Stavanger*. In Norwegian. Sira-Kvina - effects on water chemistry, acidification and fish populations in river Sira.
- Enge, E. 2010: Fiskeundersøkelser i tilknytning til forsuring, restbestander og kalking i Rogaland i 2009. *Fylkesmannen i Rogaland, Miljøvern avdelingen, Notat 1-2010. ISSN-nr: 0803-0170*. In Norwegian. Summary in English. Fish surveys in connection to acidification, remain-

- der populations and lake liming in Rogaland in 2009. (County Governor of Rogaland, Environmental Division).
- Enge, E. 2011: Forsuringsstatus for Rogaland 2007 - pH-kart. *Fylkesmannen i Rogaland, Miljøvernvedelingen, Notat 1-2011. ISSN-nr: 0803-0170*. In Norwegian. Summary in English. Acidification status in Rogaland 2007. (County Governor of Rogaland, Environmental Division).
- Enge, E. and Hemmingsen, T. 2010: Modellberegninger av vannkjemiske effekter av vassdragsreguleringer - eksempel fra Sira-Kvina reguleringen. *VANN 03-2010: 333-344*. In Norwegian. Summary in English. Modelling of water chemical effects of regulation of river Sira
- Enge, E. and Kroglund, F. 2010: Population density of brown trout (*Salmo trutta*) in extremely dilute water qualities in mountain lakes in South Western Norway. *Water, Air and Soil Pollution, DOI: 10.1007/s11270-010-0722-4*
- Enge, E. and Lura, H. 2003: Forsuringsstatus i Rogaland 2002. *Ambio Environmental Consultants & County Governor of Rogaland*. In Norwegian. Acidification status in Rogaland 2002
- Hach 2003: Water Analysis Handbook. *HACH-Company, Loveland, Colorado*
- Henriksen, A. 1982: Alkalinity and acid precipitation research. *Vatten* 38: 83-85
- Hesthagen, T. 1985: Validity of the age determination from scales of brown trout (*Salmo trutta* L.). *Institute of Freshwater Research, Drottningholm. No 62*.
- Hesthagen, T., Fjellheim, A. Schartau, A.K., Wright, R.F., Saksgård, R. and Roseland, B.O. 2011: Chemical and biological recovery of lake Saudlandsvatn, a former highly acidified lake in southernmost Norway, in response to decreased acid deposition. *Science og the Total Environment* 409: 2908-2916.
- Hesthagen, T. and Forseth, T. 1998. Reversibility of acidification in Norwegian watersheds: are brown trout (*Salmo trutta* L.) populations recovering? *Verh. Internat. Verein. Limnol.* 26: 2255-2263.
- Hesthagen, T., Forseth, T., Saksgård, R., Berger, H.M. and Larsen, B.M. 2001: Recovery of young brown trout in some acidified streams in Southwestern and Western Norway. *Water, Air and Soil Pollution* 130(1-4): 1355-1360.
- Hesthagen, T. and Jonnson, B. 1998: The relative abundance of brown trout in acidic softwater lakes in relation to water quality of tributary streams. *Journal of Fish Biology* 52: 419-429.
- Hesthagen, T., Sevaldrud, I.H., Berger, H.M. 1997: Assessment of damage to fish populations in Norwegian lakes due to acidification. *Manus in: Hesthagen, T. 1997: Population responses of Arctic char (*Salvelinus alpinus* L.) and brown trout (*Salmo trutta* L.) to acidification in Nor-*

wegian inland waters. PhD thesis, Norwegian University of Science and Technology

Huitfeldt-Kaas, H. 1922: Om aarsaken til massedød av laks og ørret i Frafjordelven, Helleelven og Dirdalselven i Ryfylke høsten 1920. *Norges Jæger og Fiskerforenings Tidsskrift* 51: 37-44. In Norwegian. About the massive fish death in the rivers Frafjordelven, Helleelven and Dirdalselven in Ryfylke the autumn 1920. (Norwegian Hunter and Anglers Society Journal)

Huitfeldt-Kaas, H. 1924: Einwanderung und Verbreitung der Süßwasserfische in Norwegen mit einem Anhang über den Krebs. *Archiv für Hydrobiologie* 14: 223-314.

Iversen, A. (Ed.) 2009: Klassifisering av miljøtilstand i vann. Økologisk og kjemisk klassifiseringssystem for kystvann, innsjøer og elver i henhold til vannforskriften. Veileder 01:2009. *Trondheim 03.07.2009. Direktoratet for Naturforvaltning*. In Norwegian. Classification of environmental status in water. System for chemical and ecological classification of coastal water, lakes and rivers. (Directorate for Nature Management)

Jensen, J.W. and Hesthagen, T. 1996: Direct estimates of the selectivity of a multimesh and a series of gillnets for brown trout, *Salmo trutta*. *Journal of Fish Biology* 49: 33-40

Jensen, K.W. and Snekvik, E. 1972: Low pH levels wipe out Salmon and Trout

populations in Southernmost Norway. *Ambio* 1(6): 223-225

Lien, L., Sevaldrud, I.H., Traaen, T.S., Henriksen, A. 1987: 1000 sjøers undersøkelsen 1986. *TA-nr: TA-0624, Vol: 282/87. Statens Forurensingstilsyn*. In Norwegian. 1000 lakes survey in 1986. (State Pollution Control Authorities. English version: TA-0525)

Miller, P.S. 1994: Is inbreeding more severe in a stressful environment? *Zoo Biology, Volume 13, Issue 3: 195-208*

Nash, R.D., Valencia, A.H. and Geffen, A.J. 2006: The Origin of Fulton's Condition Factor - Setting the Record Straight. *Fisheries, Vol. 31, No 5: 236-238*

NVE.no (2012): NVE-atlas. *Norwegian Water Resources and Energy Directorates public access database (last accessed: March 2012)*

Prodöhl, P.A., Walker, A.F., Hynes, R., Taggart, J.B. and Ferguson, A. 1997: Genetically monomorphic brown trout (*Salmo trutta* L.) populations, as revealed by mitochondrial DNA, multi-locus and single-locus minisatellite (VNTR) analyses. *Heredity* 79: 208-213, DOI:10.1038/hdy.1997.144

Qvenild, T., Kleiven, E. and Hesthagen, T. 2007: Forsuring i 150 år. *Jakt & Fiske* 10-07: 74-77. In Norwegian. 150 years of acidification.

Raddum, G.G., Fjellheim, A. and Skjel-

kvåle, B.L. 2001: Improvement in water quality and aquatic ecosystems due to reduction in sulphur deposition in Norway. *Water, Air and Soil Pollution* 130: 87-98

Rosseland, B.O., Balstad, P., Mohn, E., Muniz, I.P. and Sevaldrud, I.H. 1979: DATAFISK-SNSF-77. SNSF-project. *Technical Note 45/79*. In Norwegian. Fish population studies.

Sevaldrud, I. and Muniz, I.P. 1980: Sure vatn og innlandsfiske i Norge. Resultater fra intervjuundersøkelsene 1974-1979. SNSF-project, IR77/80. In Norwegian. Summary in English. Acid lakes and inland fisheries in Norway. Results from interviews from 1974-1979.

Skartveit, A. 1980: Observed relationships between ionic composition of precipitation and runoff. pp 242-243 in: Drabløs, D. and Tollan, A. (Eds) 1980: *Ecological impact of acid precipitation*. (Int. conf. SNSF-project, Sandefjord 1980)

Wathne, B.M. and Rosseland, B.O. (Eds) 2000: MOLAR Final Report 4/1999. Measuring and modelling the dynamic response of remote mountain lake ecosystems to environmental change: A programme of Mountain Lake Research - MOLAR. NIVA, Report nr. 96061-1