

Temporary Increase in Sea Salt Deposition Accelerates Recovery of Brown Trout (*Salmo Trutta*) Populations in Very Dilute and Acidified Mountain Lakes

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Abstract We studied the recovery of brown trout populations from 1970 to 2010 in acidified mountain lakes with low ionic content in southwestern Norway. A total of 181 test fishing surveys with gill net series were performed in 59 lakes. We found that the most significant recovery occurred during the 1980s and early 1990s. In this period, only limited improvement in the water chemistry related to acidification, i.e., pH, was observed. However, due to a temporary increase in sea salt deposition, water conductivity almost doubled during this period. In many of the mountain lakes in the study area, the brown trout populations are restricted by ion deficit. Moreover, greater ionic strength ameliorates the effects of acidification by increasing the tolerance to H^+ . Well-established relationships between conductivity and the relative abundance of brown trout (CPUE) explain the observed recovery. We conclude that the dynamics of the sea salt ion contribution should be taken into consideration wherever biological recovery in very diluted water qualities is being evaluated.

Keywords Brown trout · Sea salt deposition · Conductivity · Acidification · Recovery · Climate change

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1 Introduction

For several decades, the acidification of surface waters has been very severe in parts of the Nordic countries and North America (Schofield 1976). In Norway, the first signs of possible damage to brown trout (*Salmo trutta* L.) populations due to acidification were observed as early as in the late 1800s (Dahl 1921; Huitfeldt-Kaas 1922). However, the most extensive fish losses in Norwegian waters due to acidification occurred in the 1960s and 1970s (Hesthagen et al. 1999). Damage was first seen in mountain lakes in southern and southwestern Norway, where waters naturally have very low ionic content (Sevaldrud and Muniz 1980).

During the past three decades, the emissions of acidic components in Europe have been considerably reduced, due to a number of international emission control agreements (unece.org 2016). The first of these agreements, the 1979 Geneva Convention, entered into force in 1983. Water chemistry recovery is a slow and delayed process (Rasmussen et al. 1995). Thus, no significant improvement of the surface water chemistry related to reduced acidification was documented in the 1980s and early 1990s in southern Norway, despite the reductions in the emissions (Newell and Skjelkvåle 1997). In the following years, these emission reductions led to a pronounced improvement in water quality through higher pH values and lower concentrations of inorganic toxic aluminum (Skjelkvåle 2011; Hesthagen et al. 2011). In recent years, there has been a corresponding recovery of fish populations, which has been attributed to the improved water quality (Hesthagen et al. 2011).

In spite of the reduced deposition of acidic components, severe acidification episodes have been occasionally observed in southwestern Norway during the last two–three decades. These episodes were associated with exceptionally large sea salt depositions, caused by powerful storms (Hindar et al. 1994; Hindar and Enge 2006). A severe fish kill was observed throughout southwestern Norway in February 1993 due to this effect (Hindar et al. 1994; Barlaup and Åtland 1996). When highly Na-enriched water percolates through the soil, H^+ and Al^{3+} are mobilized due to ion exchange processes, causing highly toxic runoff water from catchments. However, the fact that a steady and moderate deposition of sea salts does not cause such adverse effects and may have a positive effect on fish populations through increasing the ionic strength of the water, has received very little attention. In the most dilute waters, which include many high mountain lakes in southwestern Norway, the distribution of brown trout is currently restricted by ion deficit rather than acidity (Enge and Hesthagen 2016). The brown trout populations in these mountain areas survive solely due to traces of airborne sea salts.

Of special importance in an acidification context is the rise in H^+ tolerance of fish as the ionic strength of the water increases. Hutchinson et al. (1989) observed a considerable improvement in survival rates of lake trout fry (*Salvelinus namaycush*) in dilute moderate acidic water by the addition of even very small quantities of NaCl. Bua and Snekvik (1972) considerably improved the hatching of brown trout in acidic water by adding neutral salts such as $CaCl_2$, $MgSO_4$, and NaCl. This is also demonstrated at population level. Muniz and Leivestad (1980) observed that a pH of >5.8 was required to ensure brown trout populations in the lakes having conductivity $<10 \mu S cm^{-1}$, while a pH value of 5.0 was sufficient at conductivities $>30 \mu S cm^{-1}$.

The conductivity of surface waters varies highly from one year to another, especially in those mountain areas where airborne sea salts are the major source of ions. This study examined the recovery of brown trout populations in 59 lakes in southwestern parts of Norway between 1970 and 2010, taking both the declining acidification and variations in conductivity into account.

2 Study Area

The study sites are located in mountain areas within the counties Rogaland, Aust- and Vest-Agder (Fig. 1). The

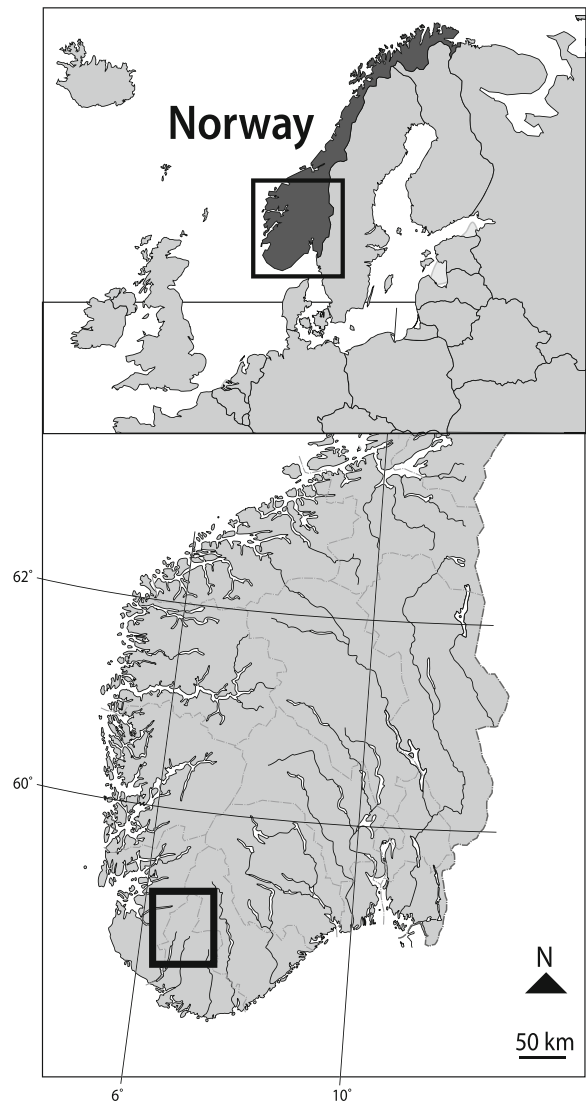


Fig. 1 The study area in southwestern Norway, indicated with a black square

bedrock in this area is primarily of Precambrian origin; gneisses and granite. These rock types include very slow weathering minerals, and their contribution of ions to water and their acid-neutralizing effect are limited. The study lakes are located at an altitude of between 49 and 971 m a.s.l., but drains watersheds up to an altitude of 1434 m. Forest vegetation reaches an altitude of about 500 and 700 m a.s.l. in the western and eastern parts of the study area, respectively. The areas on the mountain plateaus, located between the main valleys, are characterized by barren rock with limited vegetation.

The annual mean temperature and precipitation at a station located in the valley bottom, i.e., at Tjørhom, at

500 m a.s.l., are 3.2 °C and 1760 mm, respectively. At Maudal (311 m a.s.l.) the annual precipitation is 2818 mm. However, hydrological maps suggest that precipitation on the mountain plateaus is considerably higher. Upstream of Degevatn (825 m a.s.l.), the specific runoff is about $120 \text{ l sec}^{-1} \text{ km}^{-2}$ (nve.no 2016), equivalent to annual precipitation close to 4000 mm. The annual average April snow accumulation at Tjørhom is 290 mm as water equivalent (Sira-Kvina Power Company, unpublished data). At Auråhorten (1200 m a.s.l.), located in the northern part of the study area, the annual snow accumulation is 1420 mm.

All the study lakes formerly supported brown trout populations. Only a few populations have been entirely lost, while most of the remainder have been severely damaged. In the early 1970s, brown trout were stocked in many lakes that have been regulated for hydroelectric power production. However, due to the acidic water, these stockings usually failed (Gunnerød et al. 1981; Møkkelgjerd and Gunnerød 1985). The stocking programs were therefore terminated in some of the lakes, while in others, brown trout were replaced by the acid-tolerant brook trout (*Salvelinus fontinalis*). In a very few lakes, stocking of brown trout continued. These stockings were gradually reduced in course of the years and mostly came to an end in the 1990s. In some of the lakes, liming projects have been in operation during the study period, and any subsequent fish surveys in these lakes were excluded from our study. About 40 % of the lakes are regulated, with an amplitude between 1.3 and 50 m.

3 Material and Methods

3.1 Test Fishing

In the selection of data for this study, the following criteria were applied: (1) mountain lakes in the counties of Rogaland, Vest-Agder, and Aust-Agder, (2) only lakes, sensitive to acidification, (3) only lakes that were test fished twice or more during the study period 1970–2010, and (4) only lakes unaffected by stockings, or where their effect can be recorded. Our test fishing data thus amounted to 181 surveys from 59 lakes distributed over a large proportion of the three counties (Fig. 1). In addition to the authors data ($n=61$), data from published reports from County Governor of Rogaland ($n=44$), Directorate for Wildlife and Freshwater Fish ($n=24$), Rogaland Forest Company ($n=18$), and “others” ($n=34$) were used.

The test fishing was mostly performed with Jensen series (Jensen 1977) or slightly modified Jensen series, SNSF multimesh nets (Rosseland et al. 1979), and multimesh Nordic nets (Appelberg et al. 1995). The standard “Jensen series” comprises eight nets of mesh size 21–52 mm, knot to knot, which catch brown trout primarily of lengths between 19 and 45 cm. This series is often extended by one or two fine mesh nets, normally in the range of 10–16 mm. Nordic and SNSF multimesh nets include 12 and eight segments of mesh size 5–55 mm and 10–46 mm, respectively. Some of the oldest surveys were carried out using a precursor to the Jensen series, including nets in the range of 19–45 mm. A few of the surveys were performed with other mesh combinations. However, like the standard series described above, these series have a mesh size distribution that targets brown trout in a wide range of lengths. Possible differences in catchability of the gill net series were accounted for in the statistical analysis (see later).

3.2 Compilation of Water Quality Data

Data from seven water chemistry monitoring stations (1985–2010) were compiled. The study included a total of 614 samples, and the average sampling frequency was about four samples per year. Twenty-six of the 59 study lakes lie within these monitored watersheds, and 18 of the remainder are in neighboring watersheds. These monitoring stations, which drain a total watershed of 2300 km², were regarded as sufficient to determine the surface water conductivity dynamics of this mountain area. All samples were analyzed for both pH and conductivity, while 202 samples were also analyzed for Ca and Cl. The conductivity data used in this study has consequently been adjusted for the H⁺ contribution of conductivity. The conductivity data thus reflect the concentration of dissolved salts in the water. A brief description of the water chemistry analysis methods is given in Enge (2013).

3.3 Statistical Methods

When data are gathered by a number of persons and institutions in the course of 40 years, different methods of collection cannot be avoided. The primary methodical difference concerned different gill net series and particularly to the lack of the most fine-

meshed gill nets in some series. In order to adjust for these effects, the minimum mesh size of the gill net series was included as a variable in the statistical analyses. Due to the composition of the net series, this parameter does not represent a single fine-meshed net, but normally an entire net distribution down to that mesh size. Including the net series as a variable in the statistical analysis is a method of taking into account the effects of different net series that were also used in other studies (e.g., Finstad et al. 2013).

We present a longitudinal data set as it consists of repeated test fishing results from different lakes. In addition to different numbers of test fishings and no synchronizing of the surveys, the lakes have also clearly distinct fish abundance (CPUE). In such a situation, ordinary regression methods are not applicable. In the current study, linear mixed effects (LME) modeling was applied. This is a powerful statistical tool, excellent for analyzing such complex data structure (e.g., Pinheiro and Bates 2000). Using this method, the effects of site specific parameters are automatically “lumped” into an individual constant, exclusive for the specific lake, and a common time trend for all lakes is simultaneously fitted.

A histogram (not shown) of the original CPUE data displayed a very skewed distribution. In order to improve the precision of the analyses, the data were transformed to obtain a more symmetric distribution with less spread. Numerous transformations have been suggested in the standard statistical literature (e.g., Bhattacharyya and Johnson 1977). In the current analyses, the cube root transformation was found to be suitable. According to the residuals, the LME model showed a good fit using this transformation.

The LME model used in this analysis may be expressed as: $Y_{ij} = \alpha + A_i + \beta_1 t_{ij} + \beta_2 \text{Mesh}_{ij} + \beta_3 \text{Reg}_{ij} + E_{ij}$ where t_{ij} is the year of test fishing number j in lake i ;

Y_{ij} is the cube root of CPUE in lake i in year t_{ij} ; β_1 , β_2 , and β_3 are regression coefficients for the variables year, min. mesh (minimum mesh size), and reg (regulation amplitude); and α is the intercept. The term A_i represents the individual CPUE level of each lake, which is caused by local environmental conditions. The E_{ij} represents the deviation from the regression line. Using this model, CPUE is described as a function of the three individual parameters, time, net series, and regulation amplitude. The statistical analyses were performed with “R” (R Development Core Team 2007).

4 Results

4.1 Water Chemistry

There was a slow but significant rise in pH throughout the period 1985–2010 ($p < 0.01$). pH rose by 0.09–0.59 units from the first (1985–1989) to the last sampling period (2005–2010), equivalent to 0.004–0.024 pH year⁻¹ (Fig. 2, Table 1). Conductivity gradually increased throughout the first and second 5-year periods, rising to a maximum in 1993 then declining in the following years.

Conductivity correlated highly with chloride levels ($r^2 = 0.91$, $p < 0.001$, $n = 202$), suggesting that the ions were primarily of marine origin, i.e., sea salt spray (Fig. 3). The slope of the regression line was not significantly different from the theoretical conductivity-chloride ratio in dilute seawater ($p = 0.912$). Further calculations suggested that about 70 % of the conductivity was of marine origin. When Ca was included in the regression, the correlation did not rise significantly ($r^2 = 0.91$ to 0.92). A statistical explanation is that the limited and fairly constant geological ion contribution, represented by Ca, is included in the intercept of the conductivity-Cl regression ($4.8 \pm 2.5 \mu\text{S cm}^{-1}$, $n = 202$).

Fig. 2 Five-year averages of **a** pH and **b** conductivity at seven sampling stations during the study period

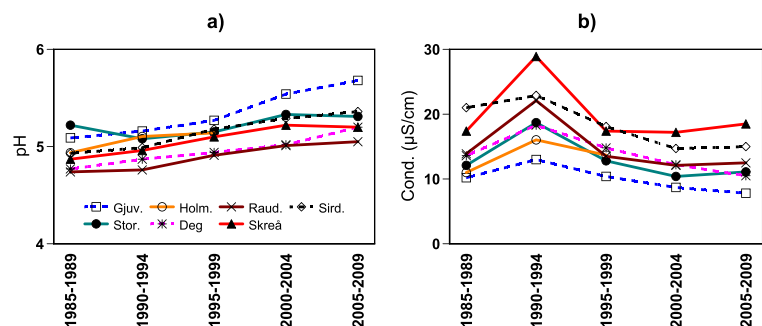


Table 1 Time series for pH and conductivity shown as 5-year averages for seven lakes. SD= standard deviation and n = number of samples

Location	Period	pH			Cond. ($\mu\text{S cm}^{-1}$)		
		Average	SD	n	Average	SD	n
Gjuvatn	1985–1989	5.09	0.14	23	10.2	4.2	21
	1990–1994	5.16	0.19	15	13.0	1.9	15
	1995–1999	5.27	0.15	18	10.4	1.5	18
	2000–2004	5.54	0.11	13	8.7	1.8	13
	2005–2009	5.68	0.08	21	7.8	0.8	21
Storstein	1985–1989	5.22	0.24	5	12.1	10.9	5
	1990–1994	5.08	0.25	14	18.7	9.6	14
	1995–1999	5.15	0.23	13	12.8	4.7	13
	2000–2004	5.33	0.16	12	10.4	4.9	12
	2005–2009	5.31	0.13	15	11.1	4.6	15
Holmevatn	1985–1989	4.94	0.09	26	11.0	3.7	26
	1990–1994	5.10	0.15	27	16.0	8.5	27
	1995–1999	5.14	0.14	12	13.7	5.0	12
	2000–2004	–	–	0	–	–	0
	2005–2009	–	–	0	–	–	0
Degevatn	1985–1989	4.77	0.12	26	13.6	4.9	23
	1990–1994	4.87	0.15	15	18.3	7.4	15
	1995–1999	4.94	0.14	19	14.8	4.5	19
	2000–2004	5.02	0.11	13	12.2	6.3	13
	2005–2009	5.20	0.14	25	10.5	3.8	25
Raudåvatn	1985–1989	4.74	0.09	34	13.9	3.6	27
	1990–1994	4.76	0.13	20	22.1	7.8	20
	1995–1999	4.91	0.12	20	13.5	3.9	20
	2000–2004	5.01	0.12	28	12.1	3.3	28
	2005–2009	5.05	0.16	26	12.5	3.3	26
Skreå	1985–1989	4.87	0.17	9	17.4	4.1	9
	1990–1994	4.96	0.26	12	28.9	13.6	12
	1995–1999	5.10	0.19	22	17.4	6.1	22
	2000–2004	5.22	0.30	27	17.2	5.5	27
	2005–2009	5.20	0.24	25	18.5	7.2	25
Sirdalsvatn	1985–1989	4.93	0.15	5	21.0	5.6	5
	1990–1994	4.99	0.14	11	22.9	4.5	11
	1995–1999	5.18	0.19	26	18.1	4.0	26
	2000–2004	5.29	0.15	27	14.7	2.5	27
	2005–2009	5.36	0.12	27	15.0	1.9	27

4.2 Statistical Analyses of Test Fishing Data

The LME analyses, based on data from 1970 to 2010, suggested growing fish abundance (CPUE) with time ($p < 0.05$), and a negative effect of regulation height ($p < 0.05$) (Table 2). There did not appear to be any

effect of minimum mesh size ($p = 0.545$). However, when the data from 1982 to 1997 were evaluated separately, the analyses suggested that CPUE increased with time ($p < 0.05$) and decreased as the minimum mesh size increased ($p < 0.05$) (Table 3). There was apparently no conclusive effect of regulation in this data selection

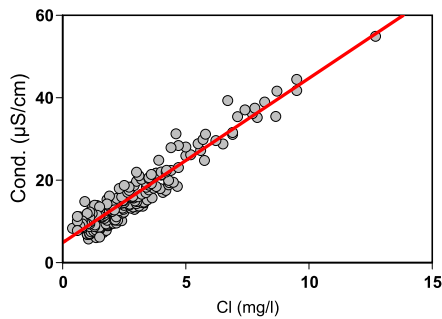


Fig. 3 Relationship between conductivity and chloride, based on data from all seven sampling stations

($p=0.064$). The estimated annual increase (time coefficient) was approximately twice as high during this period as in the period as a whole (1970 to 2010), suggesting that the most comprehensive recovery occurred during the 1980s and early 1990s. Data from the 1970s, and later than the mid 1990s, were not sufficient for separate analysis.

The fish population recovery in terms of CPUE values was especially apparent in four of the study lakes, from which data were available from six surveys throughout the period; Grauthellervatn and Håhellervatn ($p<0.05$), Ognhellervatn ($p<0.01$), and Ortevatn ($p<0.10$) (Fig. 4). The first surveys in these lakes, performed during 1972–1987, demonstrated incomplete age distributions. The surveys performed after 1995, however, showed complete age distributions, indicating healthy trout populations (Fig. 4). The effects of water chemistry were demonstrated on data from Lake Ortevatn and the inlet River Flatstølåna (Fig. 5).

5 Discussion

This study documented a comprehensive recovery of brown trout populations in the mountain lakes in southwestern Norway between 1970 and 2010. Surprisingly,

Table 2 LME analyses of CPUE data throughout the entire period from 1970 to 2010, based on 181 observations from 59 lakes

Variable	Value	Std. Error	p value
(Intercept)	−29.14	12.68	0.023
Year	0.016	0.006	0.014
Min. mesh	−0.008	0.013	0.545
Reg.	−0.018	0.008	0.022

Table 3 LME analyses of CPUE data from 1982 to 1997, based on 67 observations from 27 lakes

Variable	Value	Std. Error	p value
(Intercept)	−67.50	33.09	0.048
Year	0.035	0.017	0.039
Min. mesh	−0.034	0.016	0.045
Reg.	−0.023	0.012	0.064

the most pronounced recovery occurred during the 1980s and early 1990s, at a time when the recovery of the water chemistry from acidification had scarcely started.

On the other hand, conductivity almost doubled during the late 1980s and early 1990s (Fig. 2). Throughout the late 1990s and 2000s, conductivity levels returned to lower values than those of 1985–1989, suggesting that the values throughout this first 5-year period were already somewhat elevated. Assuming that the persistently stable levels of conductivity throughout 2000–2004 and 2005–2009 represented the “normal” conductivity level of these locations, the 1990–1994 values were temporarily 1.5–1.8 times higher, and the 1985–1989 values, 1.0–1.4 times higher than the normal values.

The primary sources of ions in freshwater are due to weathering and atmospheric input (Gorham 1961). The geology of the mountain areas in southern Norway is particularly poor as a source of ions; therefore, the atmospheric input is much more important (Wright and Snekvik 1978). The latter is highly dependant on meteorology (Gorham 1961; Hindar et al. 2004). The conductivity of the water from the current data series was primarily determined by the marine influence, i.e., the atmospheric input of sea salt spray (Fig. 3). Other surveys, partly including the current study area, confirm these findings (Enge 2013).

About 3/4 of the study lakes lie either within, or are neighboring to, the monitored watersheds. The atmospheric input of sea salt spray, causing the observed conductivity effects, is not a local effect. Since increased conductivity is recorded at seven monitoring stations draining a total area of 2300 km², we may assume that this effect somehow has affected all the lakes in the area. Data from national water quality monitoring programs also support these water chemistry findings. At Birkenes, located somewhat southeast of the study area, the annual mean values of chloride rose approximately linearly from about 3 mg l^{−1} in the mid 1980s, reaching a maximum level of 8 mg l^{−1} in 1993 (Skjelkvåle 2011). This suggests

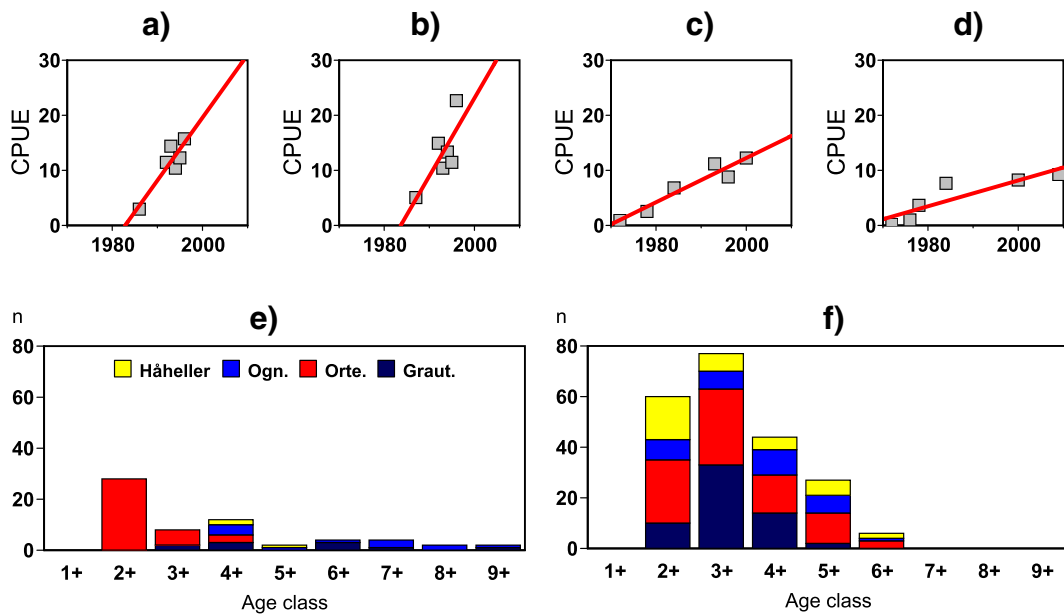


Fig. 4 Recovery (CPUE) of brown trout populations in four selected lakes: **a** Grauthellervatn ($p < 0.05$), **b** Ortevatn ($p < 0.10$), **c** Ognhellervatn ($p < 0.01$), and **d** Hähellervatn

($p < 0.05$) during the study period. The recovery in terms of the age distributions are shown in **(e)** and **(f)**, where **e** represents the first and **f** the last of the surveys in a–d

that a temporary increase in the marine ion contribution was responsible for the rise in conductivity in lakes in southwestern Norway during the 1980s and early 1990s.

A large number of studies have established the effect of ionic strength, i.e., “conductivity”, on brown trout, both at individual and population levels, especially in acidic waters (e.g., Bua and Snekvik 1972; Leivestad et al. 1976; Muniz and Leivestad 1980; Hutchinson et al. 1989; Enge and Kroglund 2011). In the most dilute water qualities of southwestern Norway, ionic strength appears to be crucial to the survival of brown trout (Enge and Hesthagen 2016). In other lakes with somewhat higher conductivity, where low ionic content is not

directly critical in itself, increased conductivity still has a pronounced positive effect by alleviating the detrimental effects of H^+ (Leivestad et al. 1976; Hutchinson et al. 1989; Enge and Kroglund 2011).

In a recent study, several scenarios of the effects of sea salt deposition on brown trout populations have been simulated, using lakes located in Rogaland County (Enge and Hesthagen 2016). This area also includes western parts of the current study area. In hypothetical scenarios, including i) removal of all sea salts and ii) a doubling of conductivity, the fraction of lakes located above an altitude of 500 m a.s.l. having a suitable water quality for brown trout ranged from i) 11 to ii) 95 %.

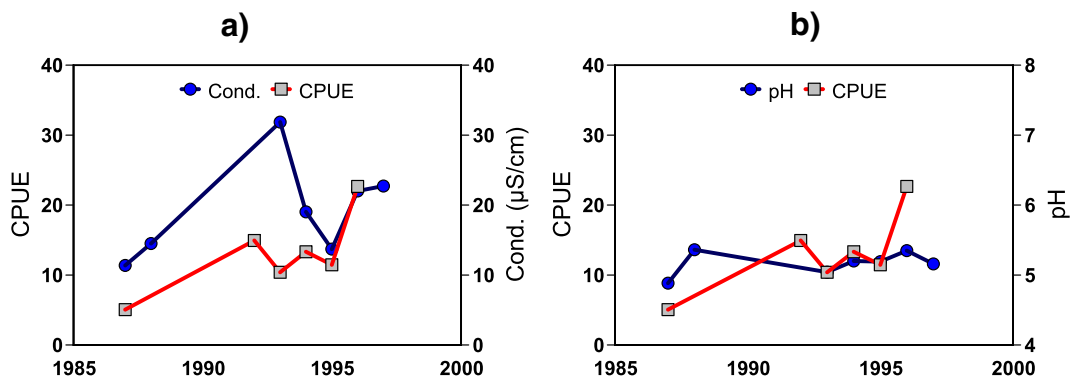


Fig. 5 Test fishing data from Lake Ortevatn and available annual averages of water chemistry; **a** conductivity and **b** pH from its main inlet river, Flatstølåna. The water chemistry axis has been scaled so as to demonstrate the relative effects of these parameters on CPUE

We conclude that a temporary increase in conductivity throughout the 1980s and early 1990s was responsible for the recovery of brown trout populations in the mountain lakes of southwestern Norway, starting more than 10 years earlier than the recovery caused by declining acidity. Not until the late 1990s and early 2000s was the recovery from acidification sufficient to have significant biological effects. The latter is basically in accordance with the recovery recorded in adjacent regions (Hesthagen et al. 2011).

The ongoing climate change will make both the positive effect of a relatively steady atmospheric sea salt contribution and the negative effects of seasalt “episodes” increasingly apparent, especially in dilute mountain waters. This study concludes that the dynamics of the marine ion contribution should be taken into account when evaluating biological recovery, especially in mountain lakes with very dilute water.

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