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Recovery of young brown trout (*Salmo trutta*) in acidified streams: What are the critical values for acid-neutralizing capacity?

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The recovery of young allopatric brown trout (*Salmo trutta*) grouped into YoY (age 0+) and older parr (age ≥1+) fish, was studied in acid-sensitive streams in a Norwegian watershed during a 24-year-period (1987–2010). Their abundance was assessed by electrofishing. Most sites typically had 5.0–5.5 in pH, 0.4–0.7 mg L^{-1} Ca, 10–20 µg L^{-1} inorganic toxic aluminum (Al_i) and acid-neutralizing capacity adjusted for organic acids (ANC_{OAA}) of - 15 to +25 µeq L^{-1}. Densities of both YoY and older parr increased significantly during the study period. Water quality also improved in recent years with respect to pH (5.8–6.0), Al_i (5–15 µg L^{-1}) and ANC_{OAA} (10–20 µeq L^{-1}). However, some negative trends in both fish density and water chemistry were found during both the first (1987–1993) and last years (2004–2008) of the study. Initially, YoY densities remained at about 16–20 specimens 100 m^{-2} (1987–1990), declined to 10–15 specimens 100 m^{-2} in the early/mid 1990s, and rosed to 30–50 specimens 100 m^{-2} in recent years (1997–2010). Their densities correlated significantly with ANC_{OAA}, and at least three stages in the recovery process were recognised: (i) Low density with 10–20 specimens 100 m^{-2} at −18 to −5 µeq L^{-1}, (ii) medium and unstable density with 20–30 specimens 100 m^{-2} at −5 to 10 µeq L^{-1}, and (iii) increasing density to 40–50 specimens 100 m^{-2} at 10–25 µeq L^{-1}. The decline in brown trout density in the early-mid 1990s coincided with high sea salt depositions, which caused increased acidification. Component 1 in a PCA explained 51% of the variation in fish densities, including conductivity, Mg, Ca, Na, alkalinity and TOC. Component 2 explained an additional 31% of the variation, including pH, Al_i and ANC_{OAA}. Multiple regression analysis coefficients showed that the two components explained 41% of the variance in total fish density. Young brown trout suffered a high mortality during the initial phase of the study in spite of relative low levels of Al_i. This is probabaly because the study streams have very diluted water. The densities of young brown trout have levelled off in recent years, indicating a development towards reaching carrying capacity and hence full recovery. However, still some annual fluctuations in density are recorded, which may be related to an unstable water chemistry.

1. Introduction

Anthropogenic emissions of sulphur and nitrogen oxides have increased the acidity of surface waters in large areas of the world, especially in eastern North America and several European countries (Rodhe et al., 1995). This process has been a major threat to biodiversity in both continents, and has also led to severe fish damage (Tammi et al., 2003; Keller et al., 2007). In Norway, water quality deterioration through acidification has severely impoverished fish communities (Hesthagen et al., 1999a). Nearly 10,000 lake-dwelling populations were extirpated during the 20th century, primarily brown trout (*Salmo trutta*).

A large number of studies have examined the relationship between survival of brown trout and various water chemistry parameters such as pH, inorganic toxic aluminium (Al_i), alkalinity and calcium (McCartney et al., 2003; Alstad et al., 2005; Kroglund et al., 2008; Malcolm et al., 2014). However, acid-neutralizing capacity (ANC) is usually used as a predictive variable in models evaluating the biological effects of acidification (cf. Driscoll et al., 1991; Malcolm et al., 2014). The lower ANC threshold needed to avoid damaged brown trout populations in acidified Norwegian lakes with 95% probability was initially 20 µeq L^{-1}, based on fish status obtained through interviews in 1986 (Bulger et al., 1993; Lien et al., 1996). ANC was at that time calculated as the difference between

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base cations and strong acid anions (*cf*. Reuss and Johnson, 1986). Later, Lydersen et al. (2004) suggested to modify ANC by assuming that the permanent anionic charge of organic acids forms part of the strong acid anions, denoted ANC_{OAA}. Using the 1986-dataset referred showed that no damaged brown trout populations was obtained at ANC_{OAA} of 8 μeq L^{-1} (Lydersen et al., 2004). It should be noted that critical values obtained from traditional ANC and ANC_{OAA} can not be directly compared. Based on a regional survey in 1995, the same protection for brown trout in clear-water lakes was achieved at ANC_{OAA} of 33 μeq L^{-1} (Hesthagen et al., 2008). In this work, probabilities for no damaged brown trout populations were also given for different TOC levels, showing that higher ANC_{OAA} values are needed to protect brown trout in more humic lakes. A higher ANC_{OAA} limit to avoid fish damage in 1995 compared with that in 1986 may be related to increased TOC content during that period (cf. Skjelkvåle et al., 2001). It has been shown that strong organic anions can contribute to the mobilization of Al_i in combination with SO_4^{2-} and NO_3^-, which is an unambiguous indication of effects of acid deposition (Lawrence et al., 2007).

Here, we analyse water chemistry and abundance of young brown trout in acidified streams in a Norwegian watershed throughout a 24-year period, from 1987 to 2010. Since 1980, the content of sulphate in precipitation at a number of sites in Norway fell by 75–91%, and by 54–81% since 1990 (Tørseth et al., 2012). This has led to that surface waters are in recovery, especially since the mid-1990s (Skjelkvåle et al., 2005; Garmo et al., 2014). However, several episodes of sea-salt depositions have occurred during the past 20–25 years, mobilizing more toxic Al (Hindar et al., 1994, 2003). Nevertheless, we expected to find a significant recovery of young brown trout relative to ANC_{OAA} during the study period.

2. Materials and methods

2.1. Study area

The study was performed in the Vikedal watershed in south-western Norway, located about 20 km from the coast (Fig. 1). The watershed covers an area of 119 km^2, which consists mainly of slowly weathering rocks such as granite and gneisses. The study was carried out at eight lakes; Fjellgardsvatn (158 m.a.s.l.), Røyravatn (230 m), Krossvatn (333 m), Djupatjern (366 m), Botnavatn (430 m), Kambetjern (464 m), Flotavatn (587 m) and Risvatn (501 m) (Fig. 1). The brown trout populations in Risvatn and Flotavatn suffered greatly from acidification during the 1980s (Hesthagen and Forseth, 1998). However, other lakes may also have acidified tributary streams with effects on young brown trout. The study sites were located above agricultural land, except for two tributary streams and the outlet of Fjellgardsvatn. None of the other streams sampled were affected by local water pollution, habitat destruction or liming. There are no roads or settlements in the cachment area above Fjellgardsvatn, except for a few small cabins. Brown trout is the only fish species in all the streams studied.

2.2. Fish sampling

Young brown trout were sampled by means of a portable back-pack electrofishing apparatus (1600 V, DC) in late August to early September each year. The water temperature generally ranged between 11 and 14 °C during the sampling. We electrofished most of the inlets, outlets and streams entering each lake. Electrofishing was not carried out above physical obstacles that might prevent brown trout from entering these sections of the streams to spawn. All localities were either sampled from or close to the shore-line of each lake, and always in an upstream direction. In each stream, we established fixed sampling areas that were repeatedly electrofished throughout the study. However, the area sampled in some of the largest inlets or outlets could vary to some extent from year to year, depending on the wetted area. The entire width of each station was generally electrofished, except in the largest inlets and outlets. Sampling station depths generally ranged from 5 to 25 cm, and their mean area ± SD was 71 ± 45 m^2. Between 20 and 24 streams were sampled each year.

The lengths of all captured fish were measured to the nearest mm. Most fish were released after sampling, except for some individuals that were removed for age determination. The fish were classified as either YoY (age 0+) or older parr (age ≥ 1+) on the basis of their length-frequency distribution in each stream. Fish in the two age classes usually ranged from 35 to 65 and 70 to 150 mm in length, respectively (Fig. 2). A total of 12 199 brown trout were caught, of which 80% were YoY (n = 9726). Older parr were mainly one-year-olds. As the sampling was carried out at the latest in early September, only very few mature fish were caught. These specimens were not included in the data-set. Each stream was sampled in a single run during the first six years of the study (1987–1992), and in three successive runs in later years (1993–2010). From the three catches in this last period, we estimated probabilities of capture (p) for both YoY and older parr (cf. Zippin, 1958; Bohlin et al., 1989). The mean p-values for these two age groups were 0.54 ± 0.06 SD and 0.68 ± 0.06 SD, respectively, and these values were used to estimate densities from 1987 to 1992.

We tested whether annual variations in environmental factors influenced the number of fish caught. To do so, we performed multiple regressions with these independent variables each year: (*i*) mean water flow during the sampling period, (*ii*) changes in water flow on days 1, 3 and 5 prior to sampling, compared to that during the sampling period, and (*iii*) water temperature, based on a mean value for all stations each year (cf. Jensen and Johnsen, 1988). The numbers of YoY and older parr caught 100 m^{-2} stream area were treated as dependent variables. Water flow measurements from the main river, River Vikedal, were used as a proxy for our study streams, using data provided by the Norwegian Water and Energy Administration. As our study streams were located in upper reaches of the watershed, data on water flow from the main river may to some extent be biased. The flow record of the river cover the full record of the study. As the variation in water flow during the study was relatively large, we ln-transformed the values for water flow to homogenize the variance of the residuals. The mean water flow (ln WF) during the sampling period each year correlated significantly with the densities of both YoY: $-8.89 * \ln WF + 49.17$, $R^2 = 0.33$, n = 24, t = −3.26, $p = 0.004$, and older parr: $-1.606 * \ln WF + 10.332$, $R^2 = 0.33$ n = 24, t = −3.31, $p = 0.003$. These equations were used to obtain values for correlating the annual catches to annual variations in water flow. This values was derived by estimating the number of fish at a mean water flow during the sampling period each year, divided by corresponding estimates of water flow. We then estimated adjusted annual catches to a mean water flow as the product of the correction value for annual variations in water flow and the original fish catch in each stream. Probabilities of capture were then utilised to estimate separate densities of YoY and older parr in each stream in individual years (Zippin, 1958; Bohlin et al., 1989). Finally, mean density was estimated for both age groups in each year.

2.3. Water chemistry

Water samples were obtained from each stream during the annual electrofishing period. Samples were analysed by standard methods, and parameters included were pH, alkalinity, major ions, conductivity, Tot-P, Si, aluminum (Al) species, total organic carbon (TOC), turbidity and water colour. Cations were

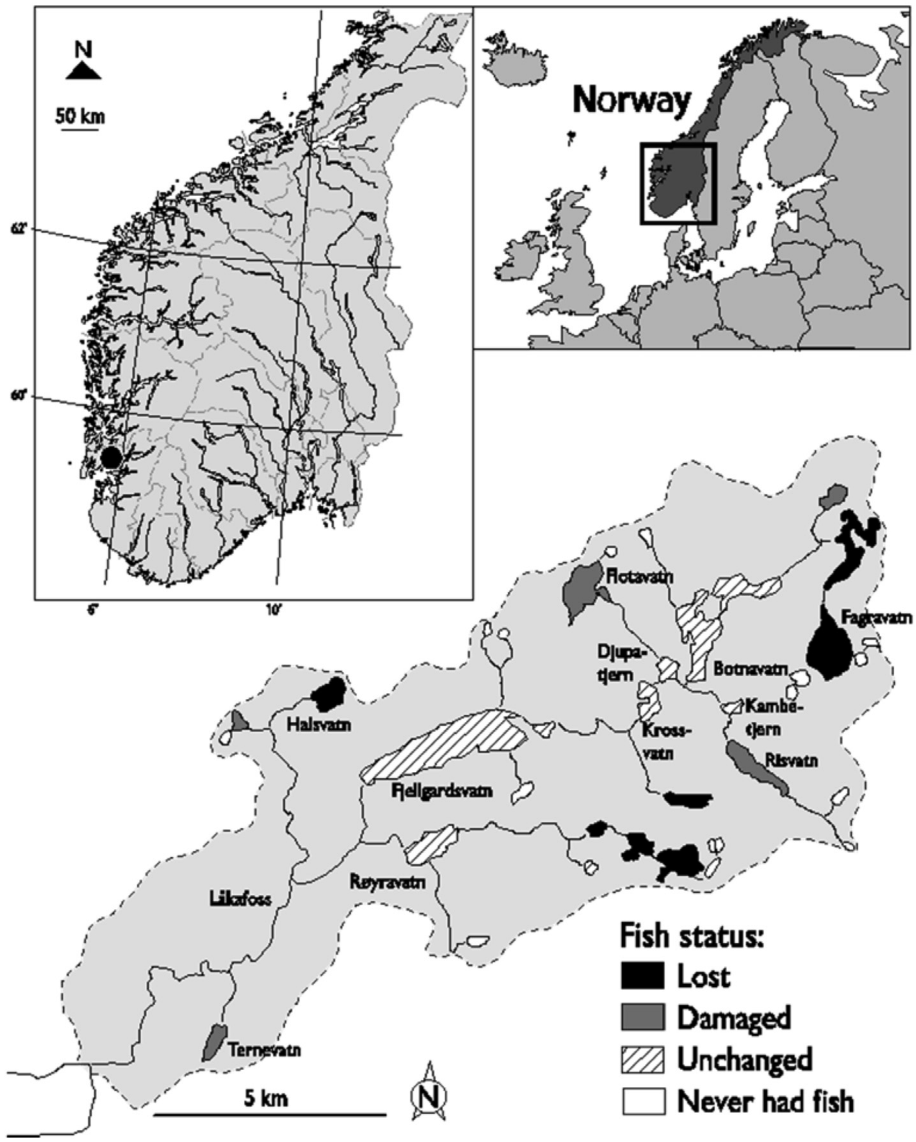

Fig. 1. Location of River Vikedal watershed with map showing the lakes whose inlets, outlets and tributary streams were sampled. Status of brown trout in each lake in the 1980s is given.

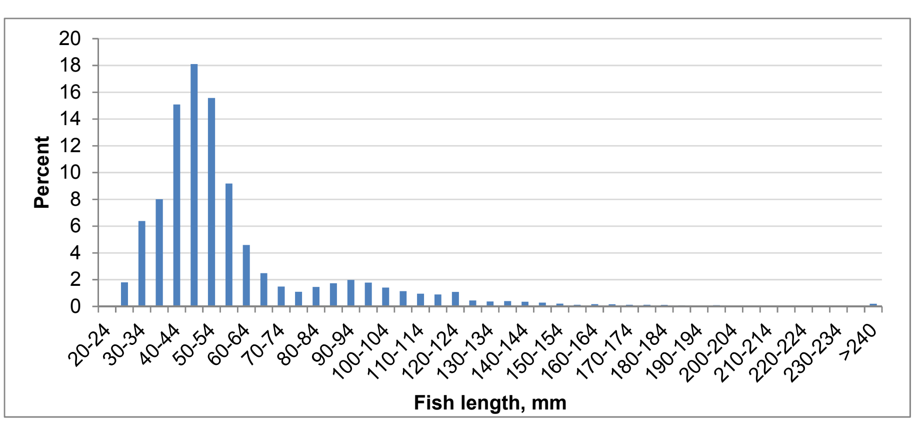

Fig. 2. Length frequency distribution of young brown trout sampled in the study streams in River Vikedal watershed between 1987 and 2010.

determined by inductively-coupled plasma atomic-emission spectrometry (ICP-AES) and anions by ion chromatography. Analysis of different Al-fractions was carried out according to Eaton et al. eds. (1995). For Al analysis, water samples were first acidified with 0.1 M HCl for 48 h to obtain Acid-reactive Al (Al_r). The remaining fractions of Al were passed through a cation exchanger before being conserved with HCl to 0.1 M. Acid-reactive Al (Al_r), total monomeric Al (Al_a) and organic monomeric Al (Al_o) were measured by means of a FIA Star model 5020, using the pyrocatechol violet method. Inorganic monomeric Al (Al_i) was then calculated from [Al_a-Al_o]. Al was not measured in 1987–1989 and in 1998–2001. The traditional ANC was calculated as the equivalent sum of base cations $[BC] = [Ca^{2+}] + [Mg^{2+}] + [K^+] + [Na^+]$ minus the equivalent sum of strong acid anions $[SAA] = [Cl^-] + [SO_4^{2-}] + [NO_3^-]$ (Reuss and Johnson, 1986). The modified ANC_{OAA}, by assuming that the permanent anionic charge of organic acids forms part of the strong acid anions, was calculated by the formula: $[BC] -([SAA] + [^1/_3 * 10.2 * TOC])$ (Lydersen et al., 2004). TOC in our study streams was measured only in 12 years (Fig. 3). In the other years, TOC was estimated from water colour (mg Pt L^{-1}): TOC = Pt colour * 1.01 + 0.70, $F_{1,258} = 614.31$, $R^2 = 0.71$, $p < 0.0001$ (n = 264). Not all cations and anions were measured in water samples collected in 1995 and from 1995 to 2001. ANC_{OAA} is therefore missing from those years results.

2.4. Statistical analysis

In order to reduce the number of variables before performing a multiple regression analysis, we performed a principal component analysis (PCA). PCA (quartimax rotation with Kaiser normalization) of the nine selected chemical variables considered to affect the survival of young brown trout yielded two principal components with eigenvalues higher than 1.00, accounting for 81% of the variation (Table 2). The two principal components were then regressed with both YoY and total fish densities using stepwise multiple regression (Tables 3 and 4). We also used the individual variables in a multiple regression analysis, and the results were broadly similar. However, since variables were highly intercorrelated, we choosed to use a PCA analysis to avoid spurious results caused by highly correlated variables.

We used the stepwise procedure in IBM SPSS Statistics with probability of F of 0.05 for entry and 0.10 for removal.

3. Results

3.1. Water chemistry

Most of the streams were acidic, with pH < 5.5, low in ionic strength with mean values of conductivity and Ca of 17.62 μS cm^{-1} and 0.60 mg L^{-1}, respectively (Table 1). The streams were also low in nutrient with 1.35 μg L^{-1} in Tot-P. They also had a low buffering capacity, with a mean alkalinity and ANC_{OAA} of 13.7 and 1.71 μeq L^{-1}, respectively. There has been a distinct improvement in water quality during the study period for pH, Al_i and ANC_{OAA} (Fig. 3). However, only minor changes if any occurred during the first years of the study (1987–1993). Thereafter, the water quality started to improve, with mean values of pH and Al_i in 1993 and 1994 of 5.2 vs. 5.6 and 23 vs. 12 μg L^{-1}, respectively. However, in 2004 a drop in pH and an increased Al_i concentration was observed, a trend which lasted until 2008. Conductivity peaked in the mid-1990s at 20–22 μS cm^{-1}, but fell again to 14–16 μS cm^{-1} in later years. On the other hand, TOC increased in recent years, with a mean ± SD value of 1.86 ± 1.03 mg L^{-1} in 1990–1996, as opposed to 3.12 ± 1.48 L^{-1} in 2007–2010.

3.2. Densities of young brown trout

Both YoY and older parr exhibited low densities during the late 1980s and early 1990s, with about 16–20 and 3–7 specimens 100 m^{-2}, respectively (Fig. 4a, b). In the mid-1990s, a pronounced decline in the density of both age groups was observed. However, there has been a significant increase in density during the entire study period in both YoY ($F_{1,22} = 70.6$, $R^2 = 0.76$, $p < 0.001$) and older parr ($F_{1,22} = 15.3$, $R^2 = 0.41$, $p < 0.001$). In recent years, mean density of these two age groups typically ranged between 35-50 and 7–11 specimens 100 m^{-2}, respectively.

3.3. A principal components analysis of water chemistry

A PCA analysis showed that conductivity, Mg, Ca, Na, alkalinity and TOC had highest loadings on component 1, which explained 51% of the variation among the nine variables included in the analysis (Table 2). Further, pH, Al_i and ANC_{OAA} had highest loading on component 2, explaining an additional 31% of the variance among the nine chemical variables. We also used these variables directly in a stepwise multiple regression analysis, which gave broadly similar results (Fig. 5). However, these variables proved to be highly inter-correlated.

3.4. A multiple regression analysis between water chemistry and fish density

Coefficients of multiple regression analysis using YoY densities as a dependent variable showed that the two components explained 38% of the variance ($R^2 = 0.38$) (Table 3). Both components were chosen in the stepwise regression procedure. We choose to present the R^2 for the model with only component 1 to show the increase in R^2 by including the other component. A model that included only component 1 explained 23% of the variance ($R^2 = 0.23$). Using total density, these two models explained 41% ($R^2 = 0.41$) and 25% ($R^2 = 0.25$) of the variance, respectively (Table 4).

pH and Al_i was positively and negatively associated with brown trout density, respectively, as shown by their sign of their loadings in the second principal component. TOC had low and opposite loadings in both principal components. Because both components correlated with trout density, TOC is probably weakly associated with their density.

3.5. Relationship between young brown trout density and ANC_{OAA}

Throughout the study period, annual mean ANC ranged from about −18 to +28 μeq L^{-1} (Fig. 6a). There was a significant correlation between YoY densities and ANC_{OAA} ($F_{1,16} = 24.7$, $R^2 = 0.61$, $p < 0.001$). Low densities with 12–22 specimens 100 m^{-2} were found in most years associated with negative ANC_{OAA} values, e.g. -20 to −5 μeq L^{-1}. Their densities started to increase when ANC_{OAA} reached positive values. However, we found large variations in fish densities at ANC_{OAA} between 0 and 10 μeq L^{-1}. At higher ANC_{OAA}, YoY densities increased more steadily although there were some exceptions, such as in 2008. A positive relationship between ANC_{OAA} and older parr densities was also found ($F_{1,16} = 19.6$, $R^2 = 0.55$, $p < 0.001$). However, their densities varied highly at ANC_{OAA} below about 10 μeq L^{-1} (Fig. 6b).

4. Discussion

There was a significant increase in the density of young brown trout as well as improved water quality in the course of the study period from 1987 to 2010. However, densities of both YoY and older

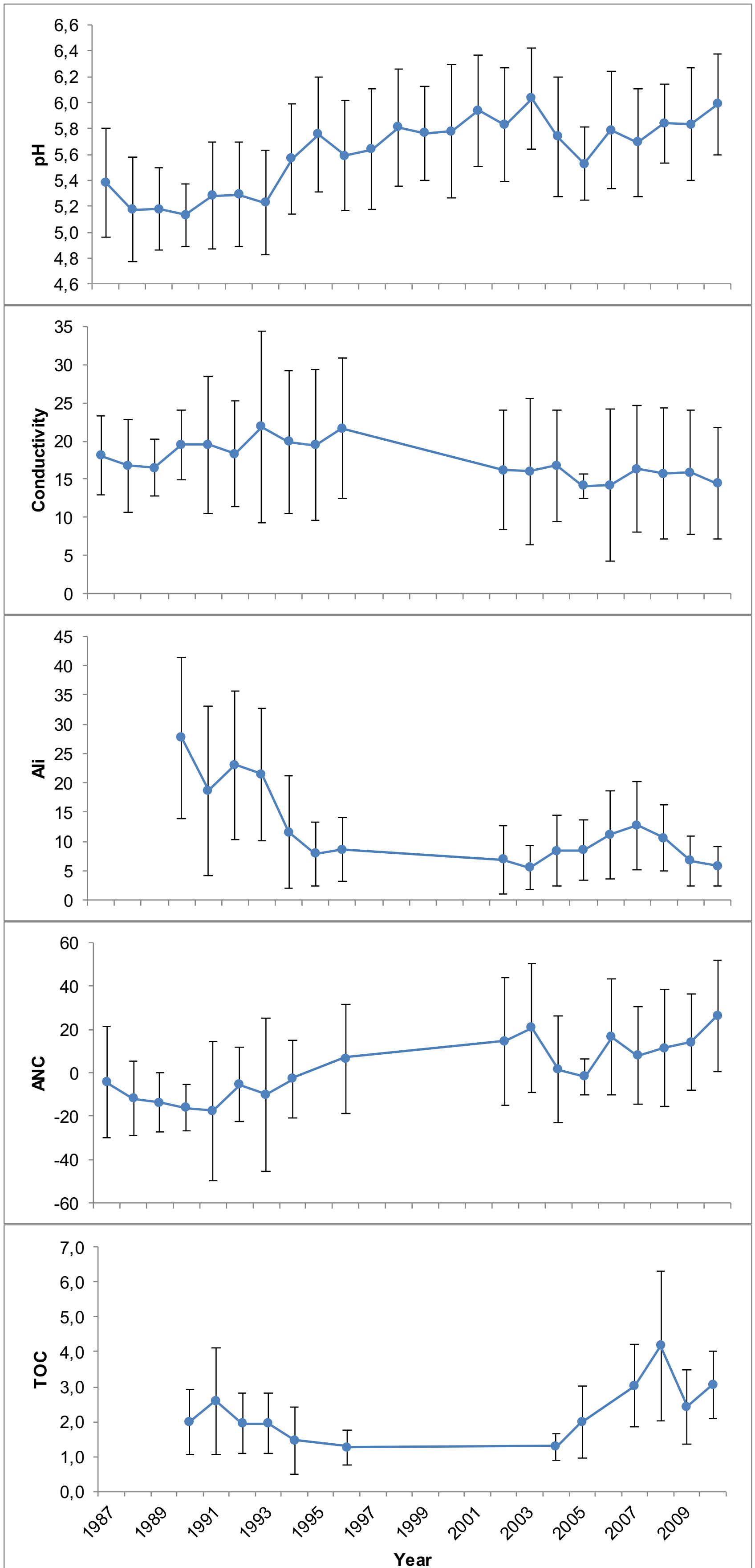

Fig. 3. Mean values ± 95% SD for pH, conductivity, Al_i, ANC_{OAA} and TOC in the study streams in River Vikedal watershed between 1987 and 2010.

Table 1
Mean values ± standard deviation (x ± SD) and range for some water chemical variables in sampled streams in River Vikedal watershed from 1987 to 2010. Measurement of water colour is given in mg Platinum (Pt) L^{-1} and that of turbidity in Formazin Turbidity Unit (FTU).

Variable	x ± SD	Range	Number	Units
pH	5.61 ± 0.49	4.65–6.97	548	
Alkalinity	13.70 ± 27.43	0–262	523	μeq L^{-1}
Ca	0.60 ± 0.69	0.15–4.49	548	Mg L^{-1}
Conductivity	17.62 ± 8.30	8.0–77.5	428	μS cm^{-1}
Mg	0.26 ± 0.16	0.10–1.16	452	Mg L^{-1}
Na	1.65 ± 0.53	0.79–4.21	452	Mg L^{-1}
K	0.18 ± 0.41	0.01–7.64	451	Mg L^{-1}
SO_4	1.84 ± 0.83	0.69–5.29	404	Mg L^{-1}
Cl	2.47 ± 1.09	0.74–8.91	404	Mg L^{-1}
NO_3	98.03 ± 182.93	0.0–1416	397	μg L^{-1}
ANC_{OAA}	1.71 ± 25.98	−48.10–136.69	396	μeq L^{-1}
Si	0.36 ± 0.28	0.02–2.15	357	Mg L^{-1}
Al_i	12.35 ± 10.65	0–54.7	357	μg/L^{-1}
TOC	2.24 ± 1.34	0.63–9.40	264	mg L^{-1}
Tot-P	1.35 ± 1.37	0.27–9.40	58	μg L^{-1}
Turbidity	0.47 ± 0.32	0–3.0	427	FTU
Colour	14.37 ± 11.60	1–92	428	Mg Pt L^{-1}

parr declined from the early to the mid 1990s. During this period, only a slight if any improvement in water quality took place. This is probably related to a large extent to the sea-salt deposition episodes in 1989, 1990 and 1993 (Hindar et al., 1994, 1995). These episodes occurred under severe weather conditions, linked to the North Atlantic Oscillation (NAO) (Hindar et al., 2002, 2003). Toxic Al mobilization was observed in several rivers in western Norway, including River Vikedal, during these episodes of sea-salt deposition. However, the severe episode in January 1993 did not seem to have caused any noticeable decline in YoY density in the autumn of that year, as opposed to its effects on older parr (cf. Fig. 4a,b). Only negligible effects on juvenile brown trout were observed that year, based on data from several other rivers in southwestern and western Norway (Barlaup and Åtland, 1996). This is probably because the eggs of that cohort were well protected in the river bed throughout the winter, while older fish were exposed to extremely toxic water. Kills of larger fish also occurred in several rivers in southern Norway in February 1993 (Hindar et al., 1994; Barlaup and Åtland, 1996).

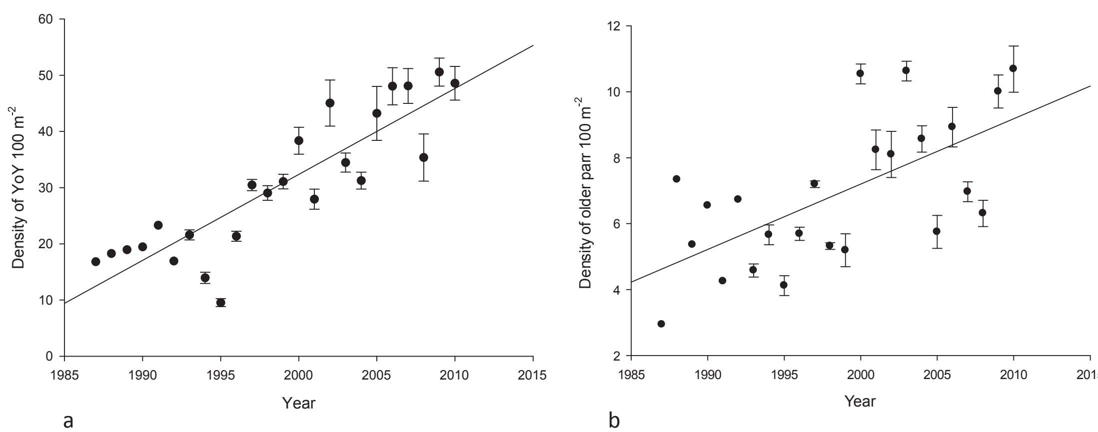

Fig. 4. Densities 100 m^{-2} ± 95% CL of YoY (a) and older parr (b) of brown trout in the study streams in River Vikedal watershed between 1987 and 2010. CL limits for 1987–1992 are not available due to one sampling run.

Table 2
Principal component analysis with eigenvalues, per cent of variance explained (rotated) and varimax rotated loadings for nine chemical variables measured from water samples taken at the time of electrofishing in the study streams.

	Component	
	1	2
Eigenvalue	4.553	2.764
% variance	51 %	31 %
Variable		
Conductivity	.980	.071
Mg	.950	..212
Na	.919	.049
Ca	.889	.398
Alk	.757	.559
TOC	.205	.-154
pH	.294	.915
Ali	.094	.-909
ANC_{OAA}	.588	-.743

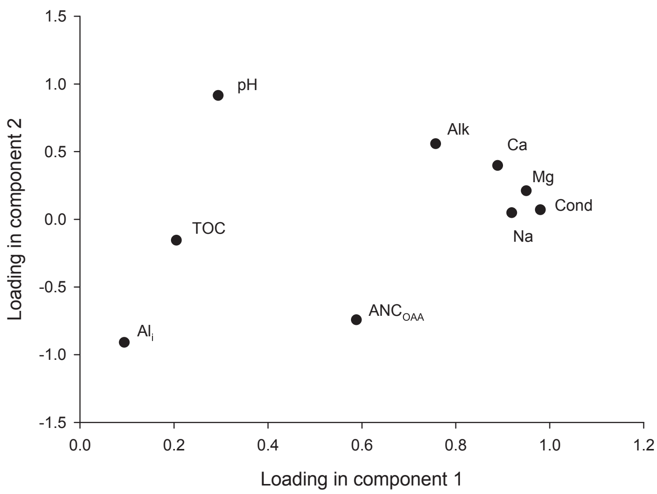

Fig. 5. Loadings of the nine water chemical variables in the two PCA-components.

Episodes of sea-salt may have dramatic effects on the water quality in runoff water. At two monitor stations located at non-forested and afforested areas in the Bjerkreim watershed south of Vikedal watershed, the concentration of Al_i increase tenfold during the sea-salt episode in 1993, to about 200 and 130 µg L^{-1}, and pH decreased from about 5.0 to 4.45 and 4.70, respectively (Hindar et al., 1995). Although both pH and Al went back to normal levels after 3–4 months, the Na/Cl-relationship in cumulated transport values indicated a long-lasting effect (>2 years) on the soil profile. Reloading the soil profile with Al and H^+ back to pre-storm values will affect the catchments ability to mobilize these ions during future sea salt episodes. This may explain the unfavourable water quality in streams in the Vikedal watershed in the early 1990s, with negative effects on young brown trout. Episodes of sea-salt deposition were also registered in 1997, 2000 and 2005 (Hindar et al., 2002, 2003; Hindar and Enge, 2006). However, the decline in water quality during these episodes was less severe in terms of causing toxic run-off water, also noticed in River Vikedal (Hindar et al., 2002). This is probably because the level of acidification has fallen in recent years (Hindar et al., 2003). This is in accordance with our results, as no significant changes in juvenile brown trout densities related to these episodes were found. Studies of sea salt episodes in different catchment types of similar sensitivity in Scotland showed also significant variations in chemical responses, especially in terms of acidification status (Harriman et al., 1995).

There was a significant relationship between ANC_{OAA} and densities of young brown trout in our study streams. The densities of young brown trout have levelled off in recent years, indicating a development towards reaching carrying capacity and hence full recovery. However, still some annual fluctuations in density are recorded, which may be related to an unstable water chemistry. Our data point to three phases in the recovery process. First, low

Table 3
Coefficients for multiple regression analysis (stepwise) of densities of YoY brown trout against the two principal components in Table 2.

Variable	Unstandardized coefficients		Standardized coefficients	t	p
	B	SE	Beta		
Constant	39.497	1.941		20.352	<0.001
Component 1	21.220	1.944	0.479	10.917	<0.001
Component 2	17.123	1.944	0.387	8.810	<0.001

Table 4
Coefficients for multiple regression analysis (stepwise) of total brown trout densities against the two principal components showed in Table 2.

Variable	Unstandardized coefficients		Standardized coefficients	t	p
	B	SE	Beta		
Constant	49.327	2.168		22.753	<0.001
Component 1	25.416	2.171	0.502	11.705	<0.001
Component 2	20.087	2.171	0.396	9.251	<0.001

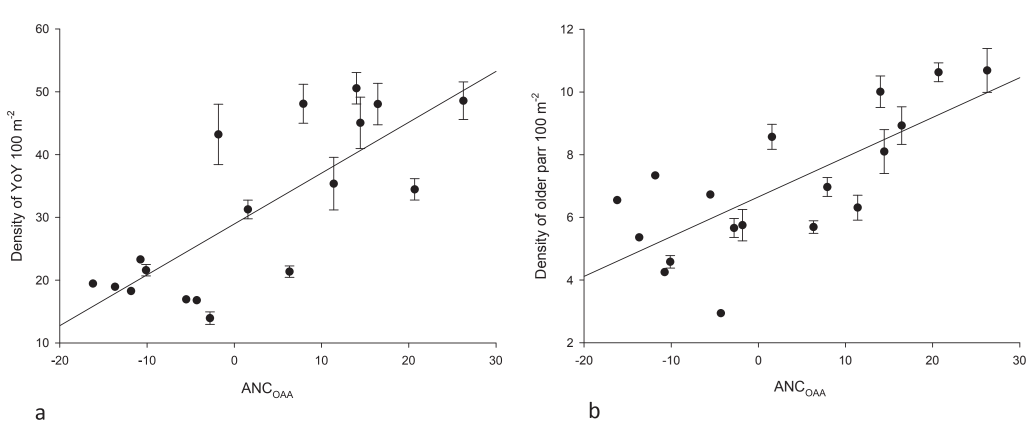

Fig. 6. Densities 100 m^{-2} ± 95% CL of YoY (a) and older parr (b) of brown trout in the study streams in River Vikedal watershed in relation to ANC_{OAA} between 1987 and 2010. CL limits for 1987–1992 are not available due to one sampling run.

densities with 10–20 specimens 100 m^{-2} at ANC_{OAA} values of about −18 to −5 μeq L^{-1}. Secondly, a stage with increased but unstable recruitment at values of 0–10 μeq L^{-1}. Thirdly, a more steady increase in density at values > 10–25 μeq L^{-1}. However, relatively large annual variations in YoY density were still evident. Thus, an ANC_{OAA} of 20–25 μeq L^{-1} seems to be necessary for significant recovery of young brown trout to take place. This ANC_{OAA} value to avoid such fish damage corresponds with that found in the inlet and outlet of an acidified lake in southernmost Norway (Hesthagen et al., 2011).

ANC_{OAA} values to protect brown trout in acidified waters has previously been estimated from regional data concerning their status in lakes obtained through interviews. Critical values to avoid fish damage deviate somewhat from that found for young brown trout in streams in the present study (cf. Lydersen et al., 2004; Hesthagen et al., 2008). These studies may be subjected to various shortcomings: (i) the evaluation of fish status is subjective, (ii) it involves mainly older and larger fish, (iii) it is restricted to lake-dwelling populations, and (iv) the water sampling did not take place at the time when the damage to the fish actually occurred. Therefore, an evaluation of ANC_{OAA} for brown trout to avoid damage should be based on young individuals in running water, and on simultaneous sampling of water. First, their early stages, which normally live in tributary streams, are regarded to be more sensitive to acidic and aluminum-rich water than older individuals, causing recruitment failure (Sayer et al., 1993; Barlaup, 1996; Hesthagen and Jonsson, 2002). Secondly, streams and rivers in acidified areas tend to have more unstable and harsher water quality than lakes. Thus, water chemistry and biology in lakes and streams should be treated separately when evaluating their recovery from acidification.

A principal component analysis identified conductivity, Mg, Ca, Na, alkalinity and TOC as the variables with highest loadings, explaining 51% of the variation. Principal component 2 had highest loading of three of the other chemical variables in the model; pH, Al_i and ANC_{OAA}, explaining additional 31% of the variance. A multiple regression analysis of the PCA components suggested that pH and Al_i were positively and negatively associated with brown trout density, because they had different signs of their individual loadings in component 2. This is consistent with an earlier study of young brown trout in streams in three acidified watersheds in Norway, also including data from Vikedal watershed (Hesthagen et al., 1999b, 2001). Al_i was not a strong indicator of acid impacts for young brown trout in the study streams, as has been found in acidified streams elsewhere (cf. Malcolm et al., 2014). In early 1990s, Al_i generally ranged between 20 and 30 μg L^{-1}, as opposed to 5–15 μg L^{-1} during recent years (2003–2010). These levels are not likely to affect the survival of salmonids in acidic water to any great extent (Kroglund et al., 2008). The effects of different water chemical variables might also be related to life stage, as small fish are more sensitive to low pH and large fish to high Al (Rosseland et al., 2001).

The reason why young brown trout have nevertheless suffered high mortality in the study streams, may be related to the diluted water. The mean concentration of Ca was 0.60 mg L^{-1}, and several of the streams had extremely low values with about 0.3–0.50 mg L^{-1}. In bioassays with pH between 4.5 and 5.4, yolk-sac fry of brown trout suffered high mortality at Ca levels of 0.25 and 0.50 mg L^{-1}, as opposed to that at 1.0 mg L^{-1} (Brown, 1983). Further, it has been shown that the Ca^{2+}: H^+ ratio is positively related to both the survival of freshly-fertilized brown trout eggs as well as to the abundance of young individuals in acidified streams (Turnpenny et al., 1987; Hesthagen et al., 1999b). This suggests that a higher calcium level is more important for their survival as acidity increases. Ion deficit might also restrict the distribution of brown trout in slightly acidic and very dilute mountain lakes (Enge and Hesthagen, 2016). Median values for conductivity and Ca in these localities were 8.7 μS cm^{-1} and 0.23 mg L^{-1}, respectively (Enge, 2013). The presence of Ca can also reduce the toxic effects of acidic and Al-rich water on other salmonids (Kroglund et al., 2008).

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