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Low Recruitment in a Population of Brook Trout in a Norwegian Watershed—Is It Due to Dilution of the Water Chemistry?

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Abstract Dilution of the water chemistry caused by reduced acidification has lately received increased attention, both in Europe and North America. There has also been a declining trend in the supply of sea salts. Several studies have predicted detrimental effects on aquatic life due to dilution. A population of brook trout living in River Hunnedal in southwestern Norway was studied for 14 years (2006–2019). Despite acceptable water chemistry with respect to pH and inorganic Al, limited reproduction was found. With median conductivity, Ca and Na of 7.1–8.6 $\mu S cm^{-1}$, and 0.17–0.19 and 0.9–1.0 $mg L^{-1}$, respectively, the water at the study sites was found to be extremely dilute. We detected a significant positive effect of Na on the densities of brook trout fry, while a less distinct effect of Ca was found. However, due to the correlation between Ca and Na we cannot conclude that Ca is unimportant. For all samplings without catch of fry ($n = 13$), Na was 0.86 ± 0.15 $mg L^{-1}$, suggesting a critical limit for Na slightly below 1 $mg L^{-1}$. We suggest that the reproduction of brook trout was restricted by the highly dilute water and the subsequent scarcity of essential ions.

Keywords Acidification recovery · Water chemistry · Dilution · Calcium · Sodium · Mountain streams · Brook trout

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1 Introduction

Acidification has caused large damage to fish population in Fennoscandian waters (Hesthagen et al. 1999; Tammi et al. 2003). However, during the past three decades, the acidification has decreased considerably, both in Europe and North America (Garmo et al. 2014). This has resulted in the recovery of fish populations in both continents (e.g., Hesthagen et al. 2016; Josephson et al. 2014). However, for aquatic life, an adverse side effect of the reduced deposition of acid compounds is reduced mobilization of base cations from the catchments, leading to a dilution of the water chemistry (e.g., Hessen et al. 2016). Among these, widespread diminishing effects on calcium in freshwaters have recently been documented worldwide (Weyhenmeyer et al. 2019). Due to the retention of base cations in the catchment associated with the restoration of the original base saturation, it has been predicted that the water chemistry will temporarily become even more diluted than in the pre-acidification state (Likens and Buso 2012). It was suggested that the chemistry may approach "demineralized water" within a few decades, based on nearly 50 years of data from "Hubbard Brook" in New Hampshire, USA. Moreover, there has also been a reduction in ionic strength in the precipitation. Based on data from 522 lakes and rivers in North America and northern Europe during the period 1990–2004, Monteith et al. (2007) found a declining deposition of sea salts. Hessen et al. (2016) found declining chloride concentrations in Norwegian lakes during the period 1986–2013. Several recent studies have predicted detrimental effects of dilution on aquatic life (e.g., Likens and Buso 2012; Enge and Hesthagen 2016; Hessen et al. 2016). Jeziorski et al. (2008) detected adverse effects on zooplankton communities and characterized the ongoing decline of calcium in freshwaters as a "widespread threat."

Brook trout (*Salvelinus fontinalis*) has been stocked into Norwegian waters due to its resistance to acidic Al-rich water (Hesthagen et al. 2018). However, less is known about their lower lethal threshold with respect to essential ions. Laboratory experiments have been performed (e.g., Hutchinson et al. 1989) but in considerably higher ionic strength water than commonly found in mountain lakes in southwestern Norway (Enge 2013).

Long-term studies of brook trout populations living in the outmost dilute waters are scarce. Here, we analyze water chemistry and abundance of brook trout in a formerly acidified Norwegian watershed during the 14 years period from 2006 to 2019. Our hypothesis is that extremely dilute water restricts reproduction of this salmonid species.

2 Study Area

The bedrock in mountain areas of southwestern Norway is comprised of slow weathering rock types such as gneisses and granite. The study area is located above the tree line, on an especially barren mountain plateau, where fish death was registered as early as late 1800s (Enge et al. 2017a). Several watersheds, including Dirdal-Hunnedal, Frafjord, and western parts of Sira (Degevatn), drain this plateau. The water chemistry is uniform and highly dilute (Enge 2013).

Our study was performed in the ultraoligotrophic Lake Hunnevatn (0.6 km^2), which is located at an altitude of 650 m a.s.l., but drains mountain areas up to 1131 m a.s.l. (Fig. 1). Lake Hunnevatn, and the two upstream lakes Tuptetjørn and Grodalstjørn, represents the uppermost lakes in the Dirdal-Hunnedal watershed.

Brown trout (*Salmo trutta* L.) is the only native fish species in this mountain area. However, most of the populations, including that in Lake Hunnevatn and the upstream lakes, became extinct due to acidification during the 1960s and 1970s (Hesthagen et al. 1999). The very last brown trout specimen reported from Lake Hunnevatn was caught during a test fishing in 1976 (Gunnerød et al. 1976).

The more acid-tolerant species brook trout was stocked in Lake Hunnevatn annually during the period 1986–2000. It established persistent populations in the lake and in the main inlet river. There has been a general decline in acidification the past decades (e.g., Enge 2013). Therefore, attempts to restore a brown trout population were initiated. In 2008, a total of 276 native brown trout, caught in the river 15 km downstream of Lake Hunnevatn, were used to stock the lake.

There has been a fluctuation in conductivity in the water from this mountain area during the past 30–40 years, as illustrated with data from the monitoring station "Degevatn" (Fig. 2), located in the neighboring watershed east of Lake Hunnevatn (Fig. 1a). Due to a high correlation between conductivity and chloride, with a slope not significantly different from the conductivity/chloride ratio in seawater, this fluctuation was attributed to sea salts effects (Enge et al. 2016). Based on the single observations from the entire period (1985–2020), there is a decreasing trend in conductivity ($p < 0.05$, $n = 141$).

3 Methods

Lake Hunnevatn was test fished in 2006 and 2015 using a standard gillnet series, comprising of 10 nets of mesh size 13.5–52 mm (c.f. Enge and Kroglund 2011). Electrofishing was performed in the inlet river during midsummer (July 26, SD ± 10 days) in 2006 and annually throughout 2010–2019 on three fixed sites (I–III) (Fig. 1b). An area of 6600 m^2 was fished, and 33 samplings were performed. Three additional sites (IV–VI) were surveyed in 2016–2019 to detect possible recruitment of brown trout and brook trout in other tributaries. However, data from these sites were not used in the statistical analysis.

The length of all fish caught by electrofishing was measured to the nearest mm, and the age was determined to 0+, 1+, or ≥ 2+ using their length distributions (see later). Due to the low number of fish caught on each site, only one fishing pass was performed. Thus, densities were estimated simply as catch (number of fish) divided by the size of the sampling area. In the statistical analyses, all fish densities were cube root transformed according to Enge et al. (2017b).

Water was sampled from each of the electrofishing sites in the inlets and from four depths (0, 5, 10, and 20 m) in Lake Hunnevatn during the fish sampling. The applied water chemistry parameters were pH,

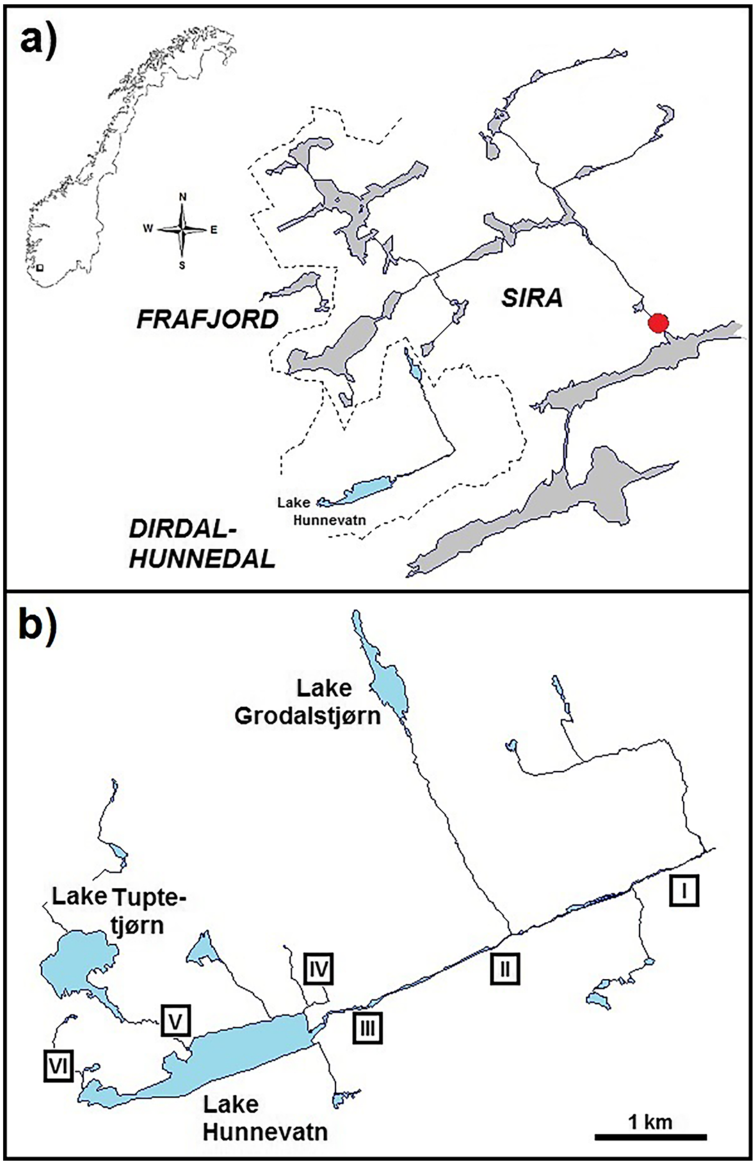

Fig. 1 Overview of the study area and the upper parts of the two adjacent watersheds Frafjord and Sira (**a**). The referred monitoring station "Degevatn" in Sira watershed is indicated with a red mark. The study sites are located in the inlets of Lake Hunnevatn (**b**)

conductivity, color, alkalinity, Ca, Na, Cl, Al (total monomeric), and LAl (inorganic toxic Al). The water chemistry analyses were performed as described in Enge et al. (2017b). Conductivity was adjusted for the H^+ contribution (c.f. Enge and Kroglund 2011). The high correlation between Na vs. Cl and alkalinity ($r^2 = 0.97$, $F_{2,27} = 490.80$, $p < 0.001$, $n = 30$) was used to estimate three missing Na values.

Quality control of analyses based on internal standards showed pH (distilled water) = 5.55 ± 0.03 (n = 51), Al (100 μgL^{-1}) = 99.5 ± 2.4 μgL^{-1} (n = 21), Na (2.14 mgL^{-1}) = 2.13 ± 0.03 mgL^{-1} (n = 46), Cl (3.86 mgL^{-1}) = 3.82 ± 0.08 mgL^{-1} (n = 50), Ca (0.32 mgL^{-1}) = 0.325 ± 0.023 mgL^{-1} (n = 40), ALK (27 μeqL^{-1}) = 28 ± 1 μeqL^{-1} (n = 38). Precision, based on duplicates, according to "Standard Methods" 1030C (Eaton et al. 1995): Conductivity: ± 0.1 μScm^{-1} (n = 25) and color: ± 1 mgL^{-1} Pt (n = 22).

As a measure of the water flow, data from the limnigraph "Jogla" in the neighboring watershed "Sira", located 17 km east of Lake Hunnevatn, was used. Snow accumulation data recorded at the snow station "Flæene" (April data), located within our study area, was received from Sira-Kvina Power Company.

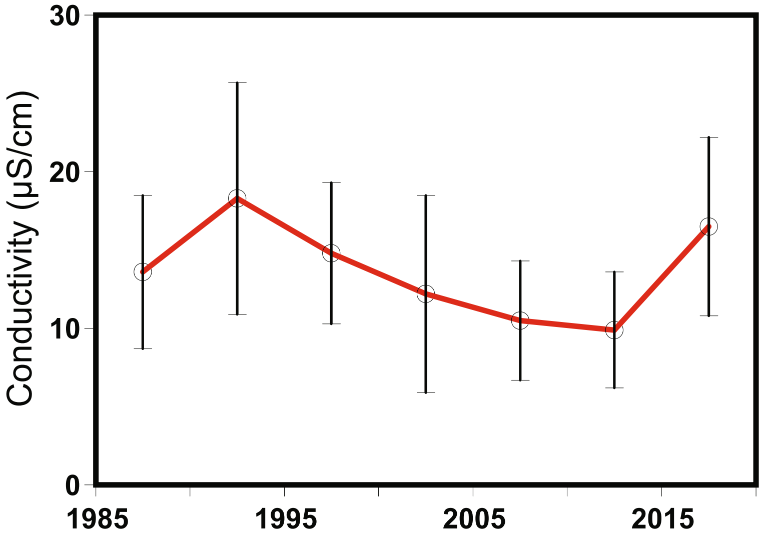

Fig. 2 Five-year conductivity averages (± SD) from the neighboring monitoring station "Degevatn." The reported data series (Enge et al. 2016) has here been prolonged with more recent data, 2010–2020 (Enge, unpublished data)

Multiple linear regressions of Ca vs. sea salt effects (Cl), flow^{-1} (dilution factor), and snow accumulation were performed in order to assess if the observed variations in Ca were long time trends or simply caused by short-time hydrological and/or meteorological variations.

Due to a high intercorrelation between many of the water chemistry parameters ($r^2_{\mathrm{MAX}} = 0.92$), i.e., not independent variables, we restricted the parameter selection in our fish density analysis to parameters strongly associated with fish physiology, which included pH, Ca, Na, and Al. Additional to these parameters, we included "color", an indirect representation of organic matter.

Data on inorganic Al ("LAl") existed only for the latter half of the observation period (2014–2019) and is therefore not included in the statistical analysis. However, inorganic Al may be complexed by organic matter (Gensemer and Playle 1999). This suggests that a combination of total monomeric Al and color may serve as a substitute for LAl. This will be demonstrated from the available LAl data from our study.

The data set consists of fish densities at the same three stations for each of the 11 years 2006 and 2010–2019. It seems reasonable that data from different (successive) years at a fixed station may be correlated. Similarly, data from different stations in a fixed year may also be correlated. There were significant correlations between stations ($r = 0.4$–0.6) and between successive periods ($r = 0.3$–0.5) when no chemical/physical parameters were included. This may corrupt the results from standard multiple regression analyses which in this situation are based on independent density data. To handle this situation, we applied simultaneous autoregressive (SAR) models (e.g., Ver Hoef et al. 2018) with maximum likelihood estimation.

To determine which of the chemical/physical parameters that were most associated with variations in fish densities, we considered every possible model with up to three parameters included as predictors. The fitted models were ranked according to the well-established AIC criterion, looking for a parsimonious model with the best possible predictive properties. Models with $\delta\mathrm{AIC} < 2$ have close to equal predictive power (Malcolm et al. 2014) and were subjected to further evaluations. These models are referred to as the "best models."

4 Results

The water sampled during electrofishing demonstrated moderate acidic water chemistry, with very low concentrations of Al and organic matter; the latter determined as "color" (Table 1). With very low values for conductivity, the water may be characterized as extremely dilute.

When accounting for the effects of flow, snow accumulation, and sea salts (Table 2), a significant decreasing trend for Ca was established in the inlet river ($p < 0.001$). This is also supported by the data from Lake Hunnevatn as median Ca values from four depths were 0.25 mgL^{-1} during test fishing in 2006 and 0.15 mgL^{-1}

Table 1 Median water chemistry from the electrofishing sites and from four depths in Lake Hunnevatn

Site (no)	Year	n	pH	Cond*	Color	ALKe	Ca	Cl	Na	Al	LAl**
				µScm^{-1}	mgL^{-1} Pt	µeqL^{-1}	mgL^{-1}	mgL^{-1}	mgL^{-1}	µgL^{-1}	µgL^{-1}
Lortabu (I)	2006–2019	11	5.65	7.1	13	8	0.17	1.0	0.9	28	(7)
Flæene (II)	2006–2019	11	5.66	8.6	8	9	0.18	1.2	1.0	27	(12)
Hunnemo (III)	2006–2019	11	5.77	8.1	7	8	0.19	1.2	1.0	22	(5)
Min-max		(33)	5.41–6.14	4.6–16.6	1–21	2–36	0.06–0.93	0.6–2.6	0.6–1.9	10–50	(2–40)
Lake Hunnevatn	2006	4	5.35	8.3	4	0	0.25	1.3	–	45	–
Lake Hunnevatn	2015	4	5.42	9.6	6	1	0.15	1.7	1.2	29	(14)
Min-max		(8)	5.16–5.50	8.2–12.3	2–7	-2-3	0.14–0.31	1.1–2.3	1.2–1.5	28–60	(14–18)

*Conductivity has been adjusted for the H^{+} contribution. **Data only available from 2014 to 2019

in 2015 (Table 1). Varying Na values were found (Fig. 3a), but no steady decline was detected during our study period ($p > 0.05$).

Calculations based on chloride established that about 60% of the conductivity originated from marine ions. Therefore, many of the parameters were highly correlated, e.g., conductivity vs. Na ($r^2 = 0.87$), Na vs. Cl ($r^2 = 0.91$), conductivity vs. Cl ($r^2 = 0.92$), and Ca vs. Cl ($r^2 = 0.50$).

Multiple linear regression demonstrated that LAl was highly correlated to “color” and total monomeric Al ($r^2 = 0.84$, $F_{2,15} = 39.16$, $p < 0.001$, $n = 18$), suggesting that the combination of these two parameters is an acceptable substitute for LAl.

The test fishing in Lake Hunnevatn in 2006 and 2015 yielded 151 and 153 brook trout, respectively, equal to a CPUE of 38 specimens per 100 m^2 gillnet area. The average fish weight was 91 and 82 g, respectively. Both the large number of fish and their small size indicated that Lake Hunnevatn was “overpopulated” with brook trout. In addition, 11 brown trout were caught in 2015 (CPUE = 3 specimens per 100 m^2) but none in 2006.

Length distribution of the fish caught by electro fishing distinguished clearly between fry (0+) and older specimen. Some overlap between age groups 1+ and ≥ 2+ may occur (e.g., 2018 data: 0+ = 45 ± 6 mm, $n = 38$; 1+ = 100 ± 11 mm, $n = 13$; and ≥ 2+ = 140 ± 13 mm, $n = 4$).

The observed densities of stream-dwelling brook trout during the study period were very low and varied considerably between years (Fig. 3b). In the inlet river, the average fish densities throughout the study period were 2.7 ± 5.0, 1.2 ± 1.2, and 1.7 ± 1.7 specimens per 100 m^2 for age groups 0+, 1+, and ≥ 2+, respectively. During the period 2014–2016, only *one* specimen of 0+ brook trout was caught, suggesting that reproduction in the river failed these 3 years. In all the seven best models for 0+ density, significant positive contribution of Na was found (Table 3). For all samplings throughout the study period, without catch of fry ($n = 13$), Na levels were 0.86 ± 0.15 mgL^{-1}. Furthermore, flowrate contributed negatively in five of these models. For density of 1+ brook trout, water chemistry was apparently of less importance. Positive effects of Na and Ca were found in four and one of the 11 best models, respectively, while no effects of physical parameters were detected. Density of older brook trout (≥ 2+) was apparently independent of any of the water chemistry parameters tested. A negative effect of flowrate was found in five of the 15 best models.

Reproduction of brook trout was also established in other brooks within our study area. At site IV, the densities of fry were especially high (55.0–68.3 specimens per 100 m^2), i.e., 20 times the fry densities in the inlet river. Brown trout fry was only detected at site IV, and the densities were low (3.8–18.6 specimens per 100 m^2).

5 Discussion

Despite a considerable variability between years, all fish densities registered at our study sites can be character-

Table 2 Multiple regression of Ca vs. sea salt effects (Cl), snow accumulation, and flow^{-1}

Step	n	ν	r^2	Significance (p)			
				Cl	Year	Snow	Flow^{-1}
1	33	28	0.708	0.001	0.001	0.419	0.703
2	33	29	0.706	0.000	0.001	0.364	
3	33	30	0.698	**0.000**	**0.000**		

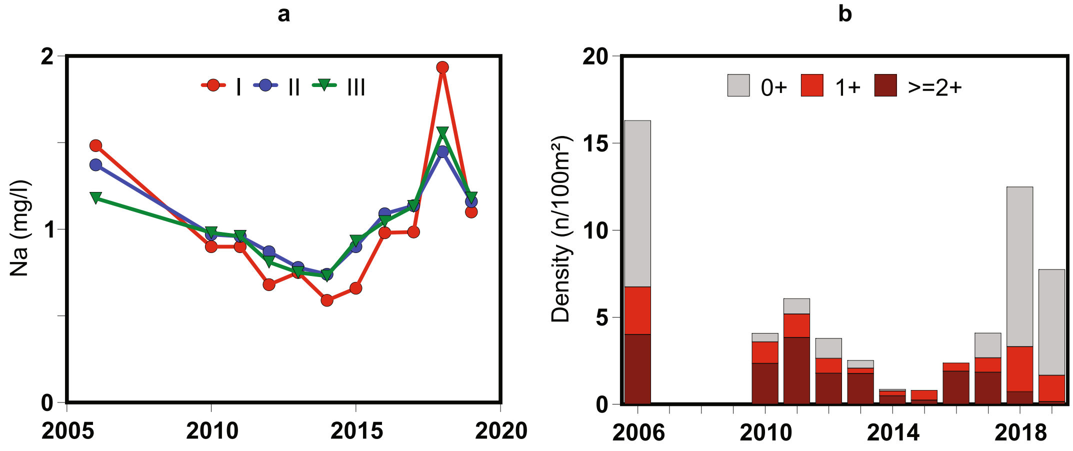

Fig. 3 Na values (**a**) from the three main sites (I–III) in the inlet river to Lake Hunnevatn. Average densities (**b**), as number of fish per 100 m^2 fishing area, for the three same locations (No data was available from 2007 to 2009)

ized as "very low." No apparent effects of "acidification parameters" such as pH and Al were detected. However, an extremely dilute water chemistry with very low concentrations of important ions such as Ca^{2+} and Na^{+} was found. Such chemistry may represent a challenge for fish (Brauner et al. 2013). From *the* possibly most dilute lake in the world (Eilers et al. 1990), two measurements of Ca were available: 0.05 and 0.10 mgL^{-1}. At our study sites, median Ca were 0.17–0.19 mgL^{-1}, and the minimum value was 0.06 mgL^{-1}.

In Lake Hunnevatn, the Ca values decreased with 0.10 mgL^{-1} between 2006 and 2015, being consistent with typical Ca declines in Norwegian lakes (Hessen et al. 2016). Decreasing Ca values were also detected in the inlet river during this study ($p < 0.001$). Declining Ca values reflects reduced mobilization of base cations from the catchment, an expected effect of declining acidification (c.f. Likens and Buso 2012). Another possible reason for lower Ca values is increased precipitation. However, data from the two nearest "official" meteorological stations, "Maudal" and "Tonstad" (Norwegian Meteorological Institute), showed no trends in precipitation throughout the current study period ($p > 0.05$). The decline in Na levels until 2014, followed by a considerable increase and thereafter a new decline (Fig. 3a), is probably due to fluctuations in the supply of marine ions, which are common in these mountain areas in coastal southwestern Norway (Enge et al. 2016). Periodically, this fluctuation causes very low levels of Na. Moreover, declining conductivity values registered at the adjacent monitoring station "Degevatn" throughout the period 1985–2020 suggest an underlying decreasing trend in the supply of sea salt. The latter is supported by data from 70 Norwegian lakes, showing declining values for chloride between 1986 and 2013 (Hessen et al. 2016). Despite considerable variations, this suggests the presence of two different negative trends: decreasing contribution of ions from the catchment (Ca) and decreasing supply of sea salt.

Acidification has declined considerably during the past two–three recent decades, both globally (Garmo et al. 2014) and regionally (Enge 2013). Additional to the *general* improvement in water chemistry, declining severity of acidic "episodes" has also been observed. In the neighboring watershed, Frafjord, draining from the same mountain plateau as Dirdal-Hunnedal (Fig. 1a), pH as low as pH = 3.9–4.2, equal to $[H^+]$ = 126–63 μM, has previously been measured during snowmelt period (Hendrey and Wright 1976). Daily sampling throughout the first half of 2011 detected two pH drops to ≈ 5.2, representing a $[H^+]$ increase of approximately + 5 μM (Enge 2012). Similar monitoring at Hompland in Sira watershed showed a minimum pH of 5.0, equal to $[H^+]$=10 μM, during snowmelt in 2009 (Enge et al. 2017b). No negative effects on fish on the adjacent electro fishing sites were detected. Daily registrations in Giljabekken, a tributary to River Dirdal 25 km downstream of Lake Hunnevatn, showed a maximum pH decrease from 6.2 to 5.6, equal to a $[H^+]$ increase of + 2 μM, during snowmelt in 2013 (Enge 2014). These three examples, all of them from our study period, and the latter from our study watershed, demonstrate that snowmelt water in this mountain area may still be acidic but currently has minimum pH values far from the critical values registered earlier.

Table 3 Regression coefficients (“x”) for parameters included in the best models (δAIC < 2)

Age	x.Na	x.Flow	x.Ca	x.Snow	x.pH	x.Al	x.Color	AIC	δAIC
0+	**1.498**	**−0.487**						60.4	0.00
	1.139	**−0.450**	(1.035)					61.0	0.57
	1.311	**−0.435**			(0.565)			61.7	1.32
	1.527	**−0.513**				(−0.009)		61.8	1.46
	1.730							62.3	1.92
	1.494	**−0.478**					(0.006)	62.3	1.92
	1.513	(−0.452)		(−0.000)				62.4	1.96
1+	**0.583**							40.0	0.00
			0.965					40.1	0.10
			(0.916)				(−0.018)	40.9	0.90
	0.557						(−0.016)	41.0	1.06
	(0.368)		(0.540)					41.4	1.43
	0.530					(0.006)		41.5	1.55
			(0.978)	(0.000)				41.6	1.66
							(−0.019)	41.8	1.87
			(0.860)			(0.004)		41.8	1.88
	(0.632)				(−0.125)			41.9	1.94
	0.576			(0.000)				41.9	1.94
≥2+		**−0.521**			(−0.781)			53.5	0.00
	(−0.565)	**−0.520**						53.8	0.37
		(−0.375)						53.9	0.45
				(−0.001)				54.2	0.74
	(−0.597)	**−0.502**				(0.009)		54.9	1.39
	(−0.328)	**−0.561**			(−0.550)			55.0	1.50
		(−0.428)		(−0.000)	(−0.749)			55.2	1.69
		(−0.352)				(0.008)		55.2	1.74
				(−0.001)			(−0.019)	55.3	1.81
		−0.520			(−0.736)		(−0.007)	55.3	1.84
				(−0.001)	(−0.454)			55.3	1.87
		(−0.249)		(−0.000)				55.4	1.88
	(−0.561)	**−0.531**					(−0.012)	55.4	1.92
		−0.503			(−0.725)	(0.003)		55.4	1.93
		(−0.390)					(−0.013)	55.4	1.97

Bold type indicates significant contribution ($p < 0.05$). Not significant ($p \geq 0.05$) is indicated with parentheses

Episodes of low pH values and high concentrations of Al may still occur, but they are normally associated with “sea salt” episodes (e.g., Hindar and Enge 2006). Extraordinary high sea salt deposition may occur during powerful storms, inducing ion exchange of Na^+ from the sea salt with and H^+ and cationic Al components from the catchment. However, such effects require that the area is acidified. In areas less affected by acidification, Na^+ is exchanged with base cations such as Ca^{2+} and Mg^{2+}. The latter effect may lead to an apparent correlation between Ca and Cl, as found in the current study ($r^2 = 0.50$). Here, the direct contribution of marine Ca was negligible (1 mg/l Cl equal 0.02 mg/l marine Ca). Therefore, decreasing acidification may also reduce the severity of sea salt episodes. This has also been demonstrated by Hindar and Enge (2006), e.g., using data from

Sira watershed. In contrary to the former "annual" pH drops during snowmelt, sea salt episodes occur with less regularity and with variable severity. Thus, we suggest that "episodes" may occasionally have effects on fish, but will not lead to general low fish densities as registered in the current study.

While the start of the snowmelt is associated with acidic water, the "tail" of the snowmelt is close to distilled water (Johannessen et al. 1980). Hendrey and Wright (1976) refer an experiment showing that water with conductivity 3 μS/cm is as lethal for brown trout fry as highly acidic snowmelt water. Therefore, when studying effects of dilute water, sampling during summer, i.e., shortly after snowmelt, is ideal. In the current study, the sampling was performed normally in late July simultaneously with the test fishing.

One fishing pass was performed in this study. Therefore, the catchability may be a crucial factor when assessing the results. Catchability decreases with decreasing conductivity. Thus, the apparent relationship between low fish density and low concentration of ions may theoretically rely on low catchability caused by low conductivity. However, three factors indicate that such conductivity effects are limited. (i) In our study, only modest variations in conductivity were observed. Average conductivity (± SD) for all stations, all years was $8.5 \pm 3.1\ \mu Scm^{-1}$, a fairly constant conductivity. Thus, the potential for variable catchability due to conductivity effects is limited. (ii) At the very lowest conductivities, the electrofishing efficiency is limited by the fish body internal conductivity, approximately 5 μScm^{-1} (Bohlin et al. 1989). In our study area, the water conductivities were approaching this limit, suggesting that other factors are more important than conductivity. (iii) Apparent lack of conductivity effects on catchability in the most dilute waters have also been confirmed by a comprehensive survey of brown trout densities in the neighboring river Sira, also having highly dilute water (Enge et al. 2017b). Here, three fishing passes were applied, and the densities were estimated according to Zippin (1958). No effects of conductivity on catchability were detected ($p > 0.05$). In total, these three factors suggest that the catchabilities were low but fairly independent on conductivity. This conclusion is also supported by visual observations. The river is shallow and has limited vegetation and extremely clear water. The years with close to no catch, young fish was hardly observed in the river.

For fry (0+), the water chemistry parameter(s) contributed significantly in all the best models, in some of the models for 1+ and in none of the models for older fish (Table 3). This may indicate a decreasing impact of water chemistry with increasing age. Another possible explanation is variable representativity of the sampled water chemistry. Water was sampled at the time of fishing, usually in July. This water chemistry is highly representative for fry as they have recently been hatched and have not been exposed to other than summer water chemistry. Older fish, on the other hand, have been exposed to variable water chemistry throughout the years(s).

Fish have the ability to avoid adverse water chemistry (Peterson et al. 1989). Fry, however, have limited mobility. Therefore, we suggest that detrimental water chemistry causes mortality of the fry rather than evasion of the detrimental water chemistry. Mobility is a possible explanation for the apparent lack of water chemistry effects on the density of older brook trout. They may have been bred somewhere else, where they were exposed to a different water chemistry.

With about 60% of the conductivity attributed to marine ions, they represent the majority of the ions in these waters. In seawater, the relative proportions of the constituents are virtually constant (Stumm and Morgan 1996). Moreover, dominant ions from the bedrock as Ca and bicarbonate ("alkalinity") appear in close to equivalent amounts (Wright and Henriksen 1978). Therefore, when using water chemistry parameters as predictor variables, here when assessing fish density, severe intercorrelation ("multicollinearity") is unavoidable. Such effects may be detected, e.g., as regression coefficient for a parameter being dependent on which other predictors are included in the model. In order to ameliorate the most pronounced effects of such intercorrelation, the parameter selection was initially restricted to those closest associated with fish physiology.

Brook trout is a highly acid-tolerant species. To impose reduced survival of eggs and fry, pH values as low as 4.2–4.4 are required (Hutchinson et al. 1989). This is 10 to 40 times more acidic water than found in our study area (Table 1). This is also about 5 times more acidic than the earlier referred snowmelt pH values from recent years. Moreover, the Al values in the inlet river were very low, with median values of total monomeric Al of 22–28 μgL^{-1} and LAl 5–12 μgL^{-1}. This is consistent with the statistical analyses, demonstrating that neither pH nor Al had any significant effect on fish densities. The apparent lack of effects of these two parameters does not imply that they are harmless, just that they were below detrimental levels. A recent study has concluded that the acidification in this mountain area is limited and that the water chemistry currently is close to "pre-acidification" state (Enge 2013). Therefore, we suggest that "acidification" no longer is a limiting factor for the brook trout in our study area.

More alarming than acidification is the highly dilute water chemistry. In the very most dilute waters, the scarcity of essential ions is in itself a critical factor for sustaining fish populations (Enge and Kroglund 2011; Brauner et al. 2013). Due to osmotic gradients, freshwater fish experience a loss of ions ("salt") to the surrounding water, which is countered by active uptake of ions (Heath 1995). In our study area, the median values for Na were about 1.0 $\mathrm{mgL^{-1}}$ (Table 1), and values as low as 0.6 $\mathrm{mgL^{-1}}$ have been measured. Even among the Amazonian fish species which, in contrary to the water chemistry "generalist" brook trout, are highly adapted to dilute waters, there are species that cannot sustain the Na balance at external values of $< 1.0\ \mathrm{mgL^{-1}}$ (Gonzalez et al. 2002). Our study established a pronounced positive effect of Na on densities of 0+ brook trout, while a less distinct effect was found for 1+ (Table 3). Na was $0.86 \pm 0.15\ \mathrm{mgL^{-1}}$ for all samplings without catch of fry. Based on this, we suggest that the critical limit for Na is slightly below 1 $\mathrm{mgL^{-1}}$ for brook trout fry.

For brown trout, availability of ions, expressed as conductivity, was a crucial factor for fry densities (Enge et al. 2017b). Due to the marine influence on the water chemistry, it was assumed that this conductivity effect was a Na effect. This is basically in line with the results from the current study, suggesting that availability of essential ions such as $\mathrm{Na^+}$ is crucial for early life stages of brook trout.

Ca plays a key role in sustaining the osmobalance, by stabilizing the gill membrane and reducing the diffusive ion loss (Gensemer and Playle 1999; Brauner et al. 2013). For the closely related brown trout, Wathne and Rosseland (2000) established that $\mathrm{Ca} = 0.38\ \mathrm{mgL^{-1}}$ is a threshold level required to sustain healthy populations. In Lake Hunnevatn, the median Ca values were 0.17–0.19 $\mathrm{mgL^{-1}}$, and values as low as 0.06 $\mathrm{mgL^{-1}}$ have been measured. In the current study, no apparent effect of Ca on densities of brook trout fry was detected, and only a weak relation to densities of 1+ was found (Table 3). In the latter models (1+), comprising Na and Ca separately, the regression coefficients were fairly constant at 0.5 and 0.9, respectively (Table 3). When both parameters appeared in the same model, the coefficients were considerably reduced. This is a typical case of multicollinearity and is most likely caused by the correlation between these two parameters (Na and Ca: $r^2 = 0.27–0.81$). Therefore, despite the apparent weak Ca effects, we cannot conclude that Ca is unimportant.

Despite apparently restricted reproduction of brook trout in the inlet river, Lake Hunnevatn is currently overpopulated with brook trout. This is probably due to two effects. First, the vast area available for spawning in the inlet river may compensate for very low densities. Secondly, besides the inlet river, reproduction has also been established in other tributaries. For brown trout, it has been established that small brooks are important refuges and may sustain relatively dense populations in lakes where the main inlet river has an unfavorable water chemistry (Hesthagen and Johnsson 1998).

High "visible" activity of brook trout in large pools in the inlet river suggests that the presence of adult fish is greater than expected, considering the very low densities of younger specimens. Due to a modest slope, 18 m on 4 km, fish can easily migrate upstream from Lake Hunnevatn. Indications of such migration are present in the current data material (Fig. 3b). In 2016 and 2017, older fish (≥ 2+) suddenly appeared, being inconsistent with the lack of younger fish in previous years. In an overpopulated lake, with a scarcity of food, fish will search for any available niche to feed. Subsequently, the river may occasionally be supplied with fish from the lake, rather than opposite.

Low catches of brown trout in Lake Hunnevatn suggested a very slow recovery of this species, despite acceptable water chemistry regarding parameters as pH and Al. Except for low densities of fry at site VI, reproduction has not been established elsewhere in the study area. Interspecies competition is hardly the reason for this. Brook trout cannot withstand the competition from brown trout (c.f. Hesthagen et al. 2018).

We suggest that very low fish densities are linked to the highly dilute water, primarily to critical low values of Na and possibly also Ca. No effect of typical acidification parameters such as pH and Al is found. Due to the apparent supply of older fish from the lake, we suggest that the river population of brook trout will not cease due to the ongoing dilution, but periodically fluctuate at very low levels. Future water chemistry development is unsure. Restoring the base cation saturation in the soil may take decades, and the water chemistry effect of an increasingly unpredictable climate is also an uncertain factor (Wright et al. 2006).

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