

Annual growth of brown trout in alpine lakes is highly influenced by spring snow depth and ice-out day

Reidar Borgstrøm¹

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Growth of annular zones in otoliths of brown trout from the alpine lakes Litlosvatn and Kollsvatn on western part of the Hardangervidda mountain plateau have been studied during the period 2004–2021, concurrent with recordings of accumulated snow in spring and dates of ice-out. Unlike the conditions in lowland areas, years with much accumulated snow have not decreased during the last decades, and years with delayed ice break-up are still frequent, opposite the trend observed elsewhere in Europe and in North America. The annual growth of the brown trout otoliths is significantly reduced in years with much snow in April and late ice-out dates, irrespective of age of the fish, indicating that somatic growth of brown trout is considerably reduced in such years. Accumulated snow in spring and ice-out day may thus be useful parameters in predictions of fish production and potential yield in such alpine lakes.

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1. Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, PO Box 5003 NMBU, NO-1432 Ås, Norway

*Corresponding author: Reidar Borgstrøm
E-mail: reidar.borgstrom@nmbu.no*

INTRODUCTION

Brown trout *Salmo trutta* L. (1758) is the most common freshwater fish in Norway, with a distribution covering nearly the whole country (Huitfeldt-Kaas 1918). It is still the only fish species in large parts of the Hardangervidda and Jotunheimen mountain areas in southern Norway (Huitfeldt-Kaas 1918; Sømme 1941; Hesthagen & Kleiven 2021).

Air temperature seems generally to be the key variable for timing of ice break-up on lakes (Ruosteenoja 1986; Vavrus *et al.* 1996; Weyhenmeyer *et al.* 2004). In Arctic and high elevation lakes, however, depth of snow cover and ice quality are important variables for ice melting in summer (Hobbie 1984; Borgstrøm 2001). Much snow may delay ice break-up (Nöges & Nöges 2014), and thereby restrict the summer season. According to Rizzi *et al.* (2018), mean winter and spring air temperatures have shown an increasing trend in Norway since the 1990s, with a concurrent reduction in lowland areas covered by snow, and earlier ice break-ups. The duration of ice cover in lowland areas has thus decreased, as also seen elsewhere in many lowland and subalpine lakes of Europe and North America, resulting in an increasing trend in surface water temperatures during the last decades (Kainz *et al.* 2017; Caldwell *et al.* 2020). L'Abée-Lund *et al.* (2021) revealed significant and accelerating trends for earlier ice break-up, later freeze-up, and completely frozen lakes, after 1991, based on an analysis of data from 101 lakes in Norway to elucidate variation in ice phenology across time and space. Their dataset covered a considerable variation in elevation (4–1401 m a.s.l.), and

the general trend therefore seems to be an increased ice-free period, even in lakes at high elevations. No lakes from the Hardangervidda mountain plateau, except the hydropower reservoir Møsvatn, were included in this analysis. Gallagher *et al.* (2022) made a meta-analysis with data from 156 studies to gain insight into key factors shaping the effects of climate on salmonid productivity, and they suggested that future warming should increase salmonid productivity at high latitudes and elevations (especially >60°N and >1500 m a.s.l.). Even though air temperatures have increased in Norway, some inland and higher mountain regions where the winter temperature (November–March) is well below zero, may still accumulate more snow due to increased precipitation (Dyrørdal *et al.* 2013). In the subalpine lake, Øvre Heimdalsvatn, the trend during the period 1969–2009 has been a delay in date of ice-free lake surface. In the early 1970s, the first ice-free day occurred around 7 June, while at the end of the period, ice-free lake was more likely to appear six days later, on 13 June (Kvambekk & Melvold 2010), probably due to the snow conditions. During the period 1986–2000 ice-out date of Litlosvatn, a lake in western part of the Hardangervidda mountain plateau, was highly dependent on the spring snow depth, giving an inter-annual variation in date of ice-free lake with more than a month, and with a negative correlation between accumulated snow and annual growth of brown trout (Borgstrøm 2001). Since the accumulated snow cover in spring in this mountain region has been extensive in several of the years from 2000 to 2022 (www.senorge.no), time of ice break-up may still be delayed in such years, despite a trend towards higher air temperature

(Qvenild *et al.* 2018).

Scales of mature brown trout frequently show a lower age compared to the otolith age (Jonsson, 1976; Závorka *et al.*, 2014; Thaulow *et al.*, 2017), and contrary to scales, otoliths continue to form annular zones even when growth in length has ceased, although new layers are added to the otolith only as caps on either side of the central groove (Power 1978). In general, otoliths are therefore more reliable in age determination, especially of old fish. In the present study, the relationship between annual ice-out day (Julian day) during the period 2004–2021 and the width of annular zones in otoliths of brown trout have been analysed to study the relative annual growth. The chosen localities are the two neighboring lakes, Litlosvatn and Kollsvatn, in the western part of the Hardangervidda mountain plateau. It is expected that much accumulated snow in spring still influences date of ice-free lakes, which in turn may affect the annual growth of brown trout.

MATERIAL AND METHODS

The lakes Litlosvatn and Kollsvatn

The lakes Litlosvatn (60.074 °N, 7.168 °E) and Kollsvatn (60.096 °N, 7.118 °E) are situated in the upper part of the Kvenna watercourse, in the western part of Hardangervidda national park, at respectively 1170 and 1182 m a.s.l. (Figure 1). Both lakes are un-regulated. Lake data are given in Table 1. Brown trout is the only fish species in these lakes as in most lakes on the Hardangervidda mountain plateau. Several high waterfalls in all rivers from this mountain plateau prevent ascendance of fish from lower parts, and presence of brown trout is originally a result of stockings (Sømme 1941). A small waterfall near the outlet from Kollsvatn may make ascendance from the lower part of the stream and from Litlosvatn difficult.

Juvenile brown trout, in length-class 4–15 cm, have been captured by electrofishing in the near-shore littoral of the lakes in the Litlos area during July and August, including Litlosvatn and Kollsvatn. Even 0+ are occasionally captured in the lakes, and lake spawning may take place, as indicated in a headwater lake to Litlosvatn (Thaulow *et al.* 2014). With the aim to reduce population density in Litlosvatn

Table 1. Elevation, surface area, catchment area of the lakes Litlosvatn and Kollsvatn (data from <https://atlas.nve.no>), and maximum depth according to Borgstrøm (2014). m a.s.l.: meters above sea level.

Lake	Elevation, m a.s.l.	Surface area (km ²)	Catchment area (km ²)	Max. depth (m)
Litlosvatn	1170	1.53	61.62	25
Kollsvatn	1182	0.62	30.64	15



Figure 1. Geographical location of the study area on the Hardangervidda mountain plateau (Map from www.norgeskart.no)

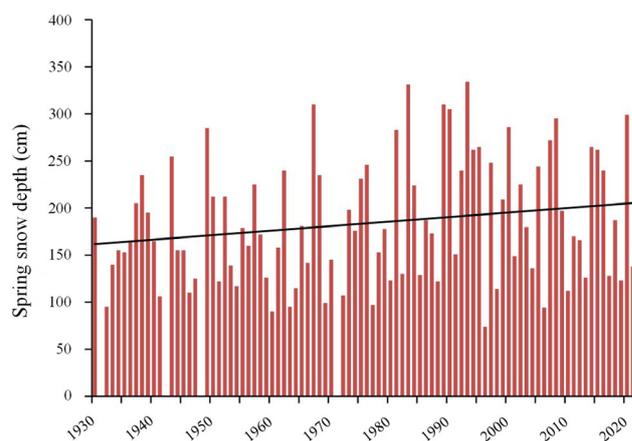


Figure 2. Measured snow depth (in cm) around 1 April at the station Litlos during the years 1930–2022, with trend line ($R^2=0.04$). Data for a few years are missing (All data from Øst-Telemarken Brukseierforening and Norsk Hydro).

and Kollsvatn, the manager of Litlos tourist lodge has performed an annual gillnet fishery with mesh sizes 24–35mm (measured from knot to knot), with highest exploitation in Litlosvatn.

The annual spring snow depth has been recorded at Litlos since 1930 by the hydropower company Øst-Telemarken Brukseierforening/Norsk Hydro, as part of the annual spring survey of snow resources in the catchment of the large Møsvatn hydropower reservoir. The snow depth measured at Litlos around 1 April has varied between 74 and 334 cm, with a high frequency of years with snow depths between 150 and 300 cm (Figure 2). During the period 1930–1980, the mean annual snow depth around 1 April has been 167 cm (s.d. ± 53 cm), while during 1981–2022 the annual average has been 203 cm (s.d. ± 71 cm), and significantly higher (t-Test, $df = 87$, $t = -2.68$, $p < 0.05$). The change in snow depth over time is however not significant (Linear regression, $df = 88$, $F = 3.48$, $R^2 = 0.04$, $p > 0.05$).

Snow and ice conditions at the lakes Litlosvatn and Kollsvatn around 1 July have been documented by photos every year from 2004 to 2022. The Norwegian Tourist Association has a staffed lodge by Litlosvatn, which is open during Easter and the summer season. Annual observations of date of completely ice-free Litlosvatn have been recorded by the hosts of this lodge during the period 1986–2021, except in the years 1999, 2001, and 2002. The snow and ice data from

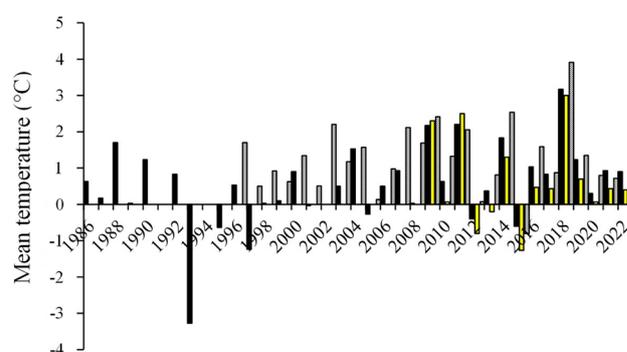


Figure 3. Mean air temperature for April–June at Finse (SN25830, 1210 m a.s.l.) 1986–2022 (black bars), Sandhaug (SN49400, 1250 m a.s.l.) 2009–2022 (yellow bars), and Tyssevatn (1330 m a.s.l.) 1996–2022 (hatched bars), all on the Hardangervidda mountain plateau (Data for Finse and Sandhaug obtained from www.seklima.met.no, and data for Tyssevatn provided by Statkraft, Tysseidal). Data from the years 1991 and 2002 at Finse are missing.



Figure 4. The partly ice-covered lakes Litlosvatn (left) and Kollsvatn, on respectively 27 July 2015 and 30 July 2015.

the lake during the period 1986–2000 have been previously published by Borgström (2001). Ice break-up on lake Kollsvatn occurs around one week after ice break-up of Litlosvatn (Jarle Viskjer, manager of Litlos tourist lodge, pers. comm.).

Mean April–June air temperature data covering the period 2009–2022 from the stations at Tyssevassbu (Figure 1), Sandhaug (c. 20 km east of Litlos), and Finse (c. 60 km north-east of Litlos), all situated on Hardangervidda, show the same general trend, with 2012 and 2015 being the coldest springs, and 2018 being the warmest (Figure 3). Mean April–June air temperature at Finse was at a minimum in 1993 (Figure 3). The ice conditions on the lakes in the year with latest ice-out day are illustrated in Figure 4, showing the northwestern part of Litlosvatn on 27 July 2015, and most of lake Kollsvatn on 30 July 2015. Temperature has been recorded continuously by TinyTag¹² loggers in Krokavassbekken (Figure 1), one of the tributaries to the lake, Kollsvatn, from July 2003 to July 2022.

Age determination and otolith measurements

Missing formation of detectable annuli in scales seems to be connected to low or no annual growth in length of fish after the first spawnings (Nordeng 1961; Jonsson 1976). Accordingly, the sagittal otoliths have been chosen for age determination of the brown trout from the two lakes. The brown trout in both lakes have practically no increase in mean length after the age of 10 years in Kollsvatn and 12 years in Litlosvatn (Figure 5). The annular widths in otoliths from a total of 36 brown trout captured in Litlosvatn and 37 captured in Kollsvatn, from end of July to middle of August in the years 2010, 2011, 2012, 2015, 2017, 2018, and 2022 have been analysed for a sequence of years and ages (Table 2). The sample from Litlosvatn consisted of fish with age 7 to 13 years, and from Kollsvatn with age 7 to 11 years. The otoliths were first cut through the centre by use of scalpel blade no. 11. One of the two otolith halves was placed on a spatula and burnt over an alcohol burner until the hyaline zones became dark brown (Figure 6). The cut and burnt otolith half was thereafter mounted in a piece of plasticine soaked in propanediol, and age determined by use of a stereomicroscope at 40x magnification. The cut surface of the otoliths were photographed by Leica DFC320 camera, mounted to the stereomicroscope. The widths of the annular zones were defined as shown in Figure 6 and measured in mm on printed photos. In practice, the otoliths did not always break through the centre, and in addition, the surface of many of the broken otoliths had to be polished by use of emery paper no. 1500 to obtain a flat surface. Because of this, the relative width of each annular zone is used in the analyses, with the

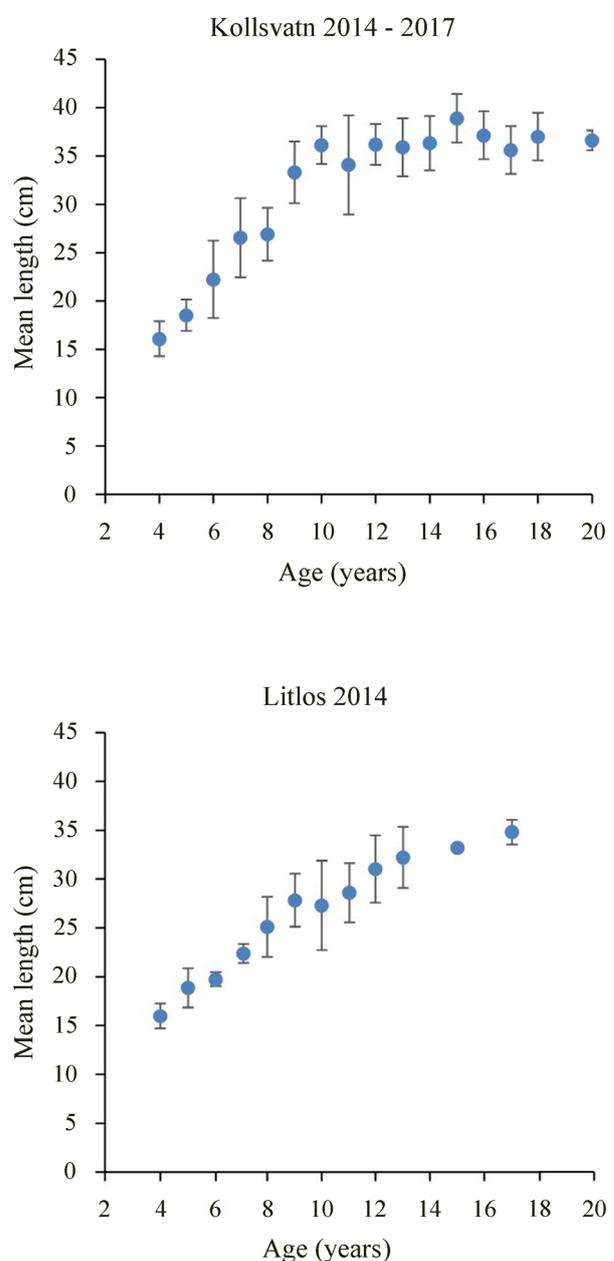


Figure 5. Mean length at age of brown trout captured in Kollsvatn, in first half of August 2014–2017, and in Litlosvatn, 28 July–16 August 2014–2016. Vertical lines indicate standard deviation.

Table 2. The sampled fish from the lakes Kollsvatn and Litlosvatn used in the annual growth analysis of the otoliths. Standard deviation given in parenthesis.

Lake	Year-class	Year of capture	Number	Mean length (cm)	Age (in winters)	Measured width of annular zone no.
Kollsvatn	2001	2010	1	32.4	9	4–8
”	«	2011	1	34.5	10	4–8
«	«	2012	2	33.4	11	4–8
«	2002	2010	3	31.1 (± 0.7)	8	3–7
«	«	2011	2	35.4	9	3–7
«	«	2012	6	33.5 (± 2.0)	10	3–7
«	2009	2018	11	31.4 (± 2.5)	9	3–8
«	2010	2017	10	26.2 (± 3.7)	7	2–7
«	2010	2018	3	30.3 (± 1.9)	8	2–7
Litlosvatn	2002	2015	13	35.7 (± 2.4)	13	3–9
«	2010	2017	6	25.7 (± 4.0)	7	2–7
«	2010	2022	3	36.0 (± 4.4)	12	5–12
«	2011	2022	6	35.5 (± 1.5)	11	4–11
«	2012	2022	4	34.7 (± 2.5)	10	3–10
«	2013	2022	3	36.0 (± 4.4)	12	2–9



Figure 6. Cut and burnt otolith of a brown trout captured in Litlosvatn, in end of July 2022, showing how the annuli are defined and the widths of the annular zones measured along an axis from centre to edge of the cross section

width of the first annular zone in each analysed sequence of age-classes set to 100.

Statistical analysis

T-tests with paired two sample for means were used to test differences in width of annual growth zones in otoliths. A linear model (function “lm”) in the statistical software R version 4.2.3 (R Core Team 2023) has been used to explain the variation in relative annual growth as a function of growth season (age), locality (Litlosvatn and Kollsvatn), ice-out day, and the interactions between growth season and locality, as well as ice-out day and locality. The main purpose of this was to investigate the effect of ice-out day while controlling for age-dependent growth, and if the ice-out effect differed between the two lakes. Linear regression in Excel was used to test the relationship between snow depth and day of ice-free lake, as well as snow depth and mean July–August temperature in Krokavassbekken, a tributary to the lake, Kollsvatn. T-test in Excel was used to test the difference in annual snow-depths before and after 1980.

RESULTS

Spring snow depth and date of ice-free lake

In years with much snow in spring, as measured at Litlos during the years 2004–2021 (Figure 2), both lakes were still partly or completely ice covered around 1 July in the years 2005, 2007, 2008, 2012, 2014, 2015, 2016, and 2020, and still with much remaining snow in the terrain (Figures 7 and Figure 8). In years with low snow depth in spring (Figure 2), there was likewise little snow in the terrain around 1 July, and with Litlosvatn and Kollsvatn both being ice-free (Figure 7 and Figure 8). First day of ice-free lake were in the range from 10 June (day 161 in 1988) to 7 August (day 209 in 2015). Throughout the period 1986–2021, ice-out day of Litlosvatn significantly followed the snow depth in April (Anova, $F=89.18$, $df=32$, $p<0.001$) (Figure 9).

Snow depth and stream temperature

Mean July–August temperature in Krokavassbekken showed large annual variations during the period 2003–2021, from a maximum at 13.4 °C in 2006 to a minimum at 3.2 °C in 2015 (Figure 10). The relationship between spring snow depth at Litlos and the mean July–August temperature in this stream was highly significant (Linear regression, $df=18$, $F=17.11$, $R^2=0.50$, $p<0.001$). The low stream temperatures in the years 2007, 2012, 2015, and 2020, coincide with much snow in the terrain both around 1 April (Figure 2) and in beginning of July during these years, as documented in Figure 8. In these years, long stretches of Krokavassbekken and the other effluent streams to Kollsvatn were covered with snow or surrounded by snow far into July.

Relative annual growth

In the otolith samples from the lakes Kollsvatn and Litlosvatn, the relative widths of the annual zones vary considerably between years (Figure 11). The annular zones laid down in the years 2005, 2007, 2012, 2015, and 2020 appear as narrower both compared with the zones in preceding and subsequent year(s), irrespective age of the fish. The widths of the annular zone of individuals in year-classes 2001 and 2002 from Kollsvatn are significantly broader at respectively age 4

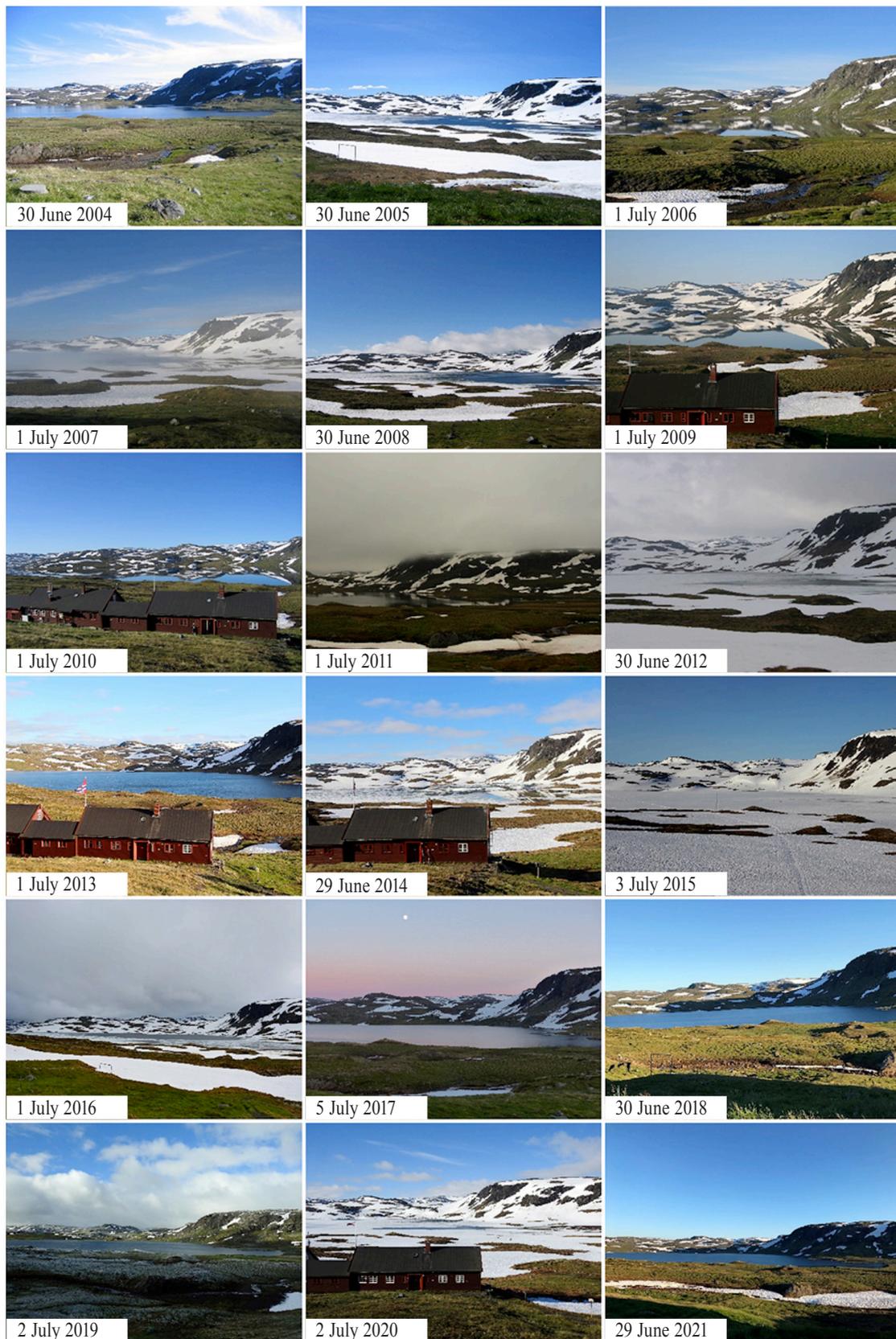


Figure 7. Photos from Litlosvatn around 1 July 2004–2021. (Photo from 2011 and 2016 by B. O. Hagen; Photo from 2021 by J. Viskjer; other photos by R. Borgstrøm)

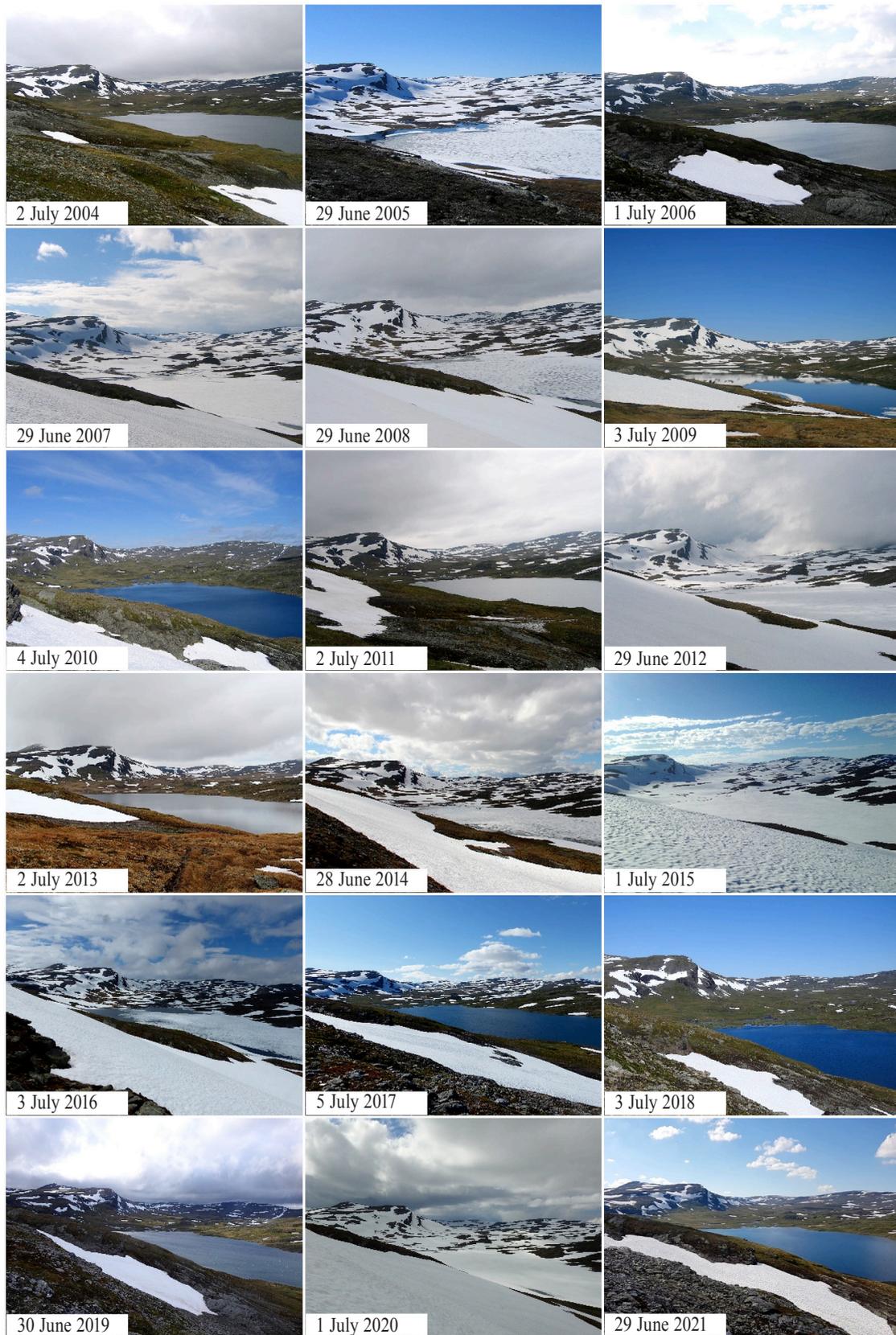


Figure 8. Photos from Kollsvatn, taken around 1 July 2004–2021. (All photos by R. Borgström, except photo from 2021, taken by O. Hilde).

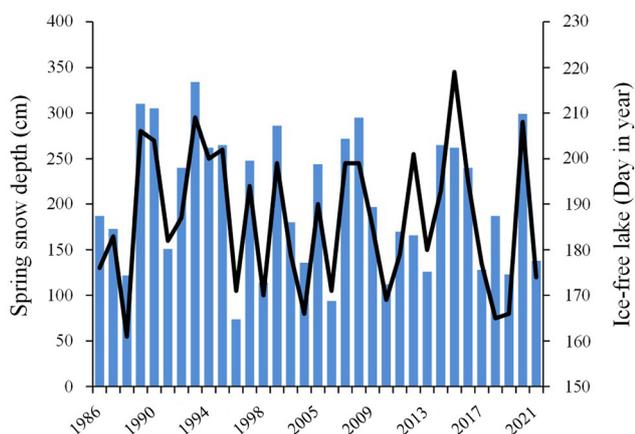


Figure 9. Spring snow depth (cm) (columns) and day in year of ice-free Litlosvatn (black line), during the period 1986–2021. NB! Ice data for the years 1999, 2001, and 2002 are missing, and these years are not included in the figure. (Snow depth data provided by Øst-Telemarken Brukseierforening and Norsk Hydro).

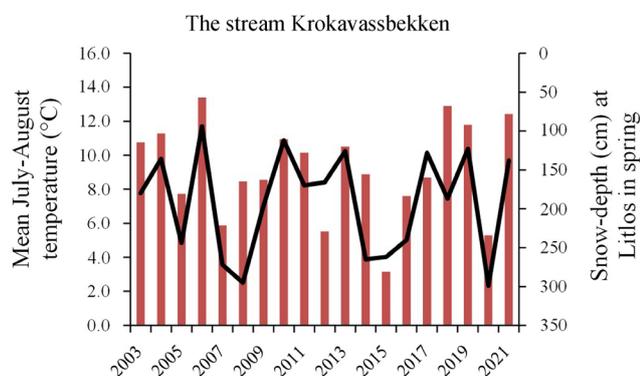


Figure 10. Mean July–August temperature in the stream Krokavassbekken (columns) and measured snow depth in spring at Litlos (line) from 2003 to 2021. (Snow depth data provided by Øst-Telemarken Brukseierforening and Norsk Hydro).

and 5 in 2006 than at age 3 and 4 years in 2005 ($t=-7.5$, $df=15$, $p<0.001$) (Figure 11A). Likewise, individuals in year-class 2002 from Litlosvatn have significantly broader annular zone at age 4 years in 2006 compared to the width in 2005, at age 3 years ($df=12$, $t=-8.8$, $p<0.001$) (Figure 11C). In the same way, individuals in year-class 2009 and 2010 from Kollsvatn and individuals in year-class 2010 from Litlosvatn have significantly broader annular zones in 2013 than in 2012 (respectively $df=24$, $t=-7.5$, $p<0.001$, and $df=5$, $t=-6.9$, $p<0.001$), and also broader zones in 2016 than in 2015 (respectively $df=24$, $t=-12.1$, $p<0.001$, and $df=5$, $t=-4.9$, $p<0.01$) (Figure 11B, D). Individuals in the year-classes 2010–2013 from Litlosvatn had significantly broader annular zones in 2016 than in 2015 ($df=16$, $t=-8.4$, $p<0.001$), and likewise significantly broader zones in 2021 compared to 2020 ($df=16$, $t=-8.1$, $p<0.001$) (Figure 11E). In all years with the narrowest annular zones, ice-out days were delayed (Figure 11), giving a significant effect of ice-out day on width of the annular zones after controlling for age-dependent deceleration of annual growth (Table 3). While the effect of ice-out day was significant in both lakes, the effect was stronger in Kollsvatn compared to Litlosvatn, with respectively 1.5% and ca 1% reduced growth for each day of delayed ice out (Table 3).

Photos of broken and burnt otoliths of brown trout from the two lakes illustrate the marked differences in widths of the annular zones

Table 3. A linear model describing the variation in relative annual growth of brown trout as a function of growth season (age), locality (Litlosvatn and Kollsvatn), ice-out day and biologically relevant two-way interactions. The model explains 80% of the variation in the data ($R^2=0.8$)

	Estimate	SE	t	p
Intercept	78.2	4.23	18.5	<0.001
Growth season (Kollsvatn)	-0.53	1.27	-0.4	0.676
Locality (Litlosvatn vs Kollsvatn)	15.6	5.27	3.0	0.0042
Ice-out day (Kollsvatn)	-1.50	0.15	-9.9	<0.001
Growth season x locality (Litlosvatn vs Kollsvatn)	-4.08	1.42	-2.9	0.0053
Ice-out day x locality (Litlosvatn vs Kollsvatn)	0.54	0.18	3.1	0.0032

between years with much snow and late ice-out day (2012, 2015, 2020) and the neighboring years (Figure 12). The annular zones formed in these years appear as much narrower than the subsequent zones, irrespective of year-class and capture year.

DISCUSSION

As indicated by the snow depth measurements in the Litlos area, years with much snow in spring have increased during the last 40 years compared with the years 1930–1980, despite a general increase in winter and spring temperatures in Norway during the last decades (Rizzi *et al.* 2018). According to the significant relationship between accumulated spring snow depth and first ice-free day of the lake, the ice break-up is delayed after springs with much accumulated snow. The early ice disappearance in the warm spring and summer 2018, seems to be an exception. The high April–June temperature on Hardangervidda this year resulted in an earlier ice-free lake than expected when based on the measured snow depth around 1 April, thus being an indicator of future conditions if air temperature continues to increase. On the other hand, the low air temperatures in April–June 2012 and 2015 resulted in later ice-free lake than expected in these years, based on the measured snow-depth in beginning of April.

As long as the fish grow in length, the width of the annular zones in otoliths and scales may correspond to the annual length increments of the fish (Nordeng 1961; Thaulow *et al.* 2017). In general, it is expected that length increment in year $t+1$ is less than in year t , because growth in length generally decreases with age (Kennedy & Fitzmaurice 1971; Ricker 1975). Exceptions to this general trend are often connected to a marked shift in habitat use and feeding conditions, typically seen in anadromous salmonids in which annual growth of juveniles is low compared to the faster growth after smoltification and migration to saltwater (Dahl 1913; Jonsson & L'Abée-Lund 1993). Likewise, annual growth of brown trout during the first years in running waters might be lower than the subsequent lacustrine growth (Dahl 1913). However, as observed in the otolith samples from the lakes Kollsvatn and Litlosvatn, the widths of the annular zones did not follow the expected growth pattern with gradually decreasing widths as fish become older, neither a typical shift from low annual growth during the first years to higher growth in older fish. Several age-classes from Litlosvatn and Kollsvatn follow the same growth pattern in specific years, with relatively narrow annular zones in the years 2005, 2012, 2015, 2020, and significantly broader zones in the subsequent year(s), indicating influence of the same growth conditions, irrespective year-class and age-class, and irrespective the age effect which otherwise would have

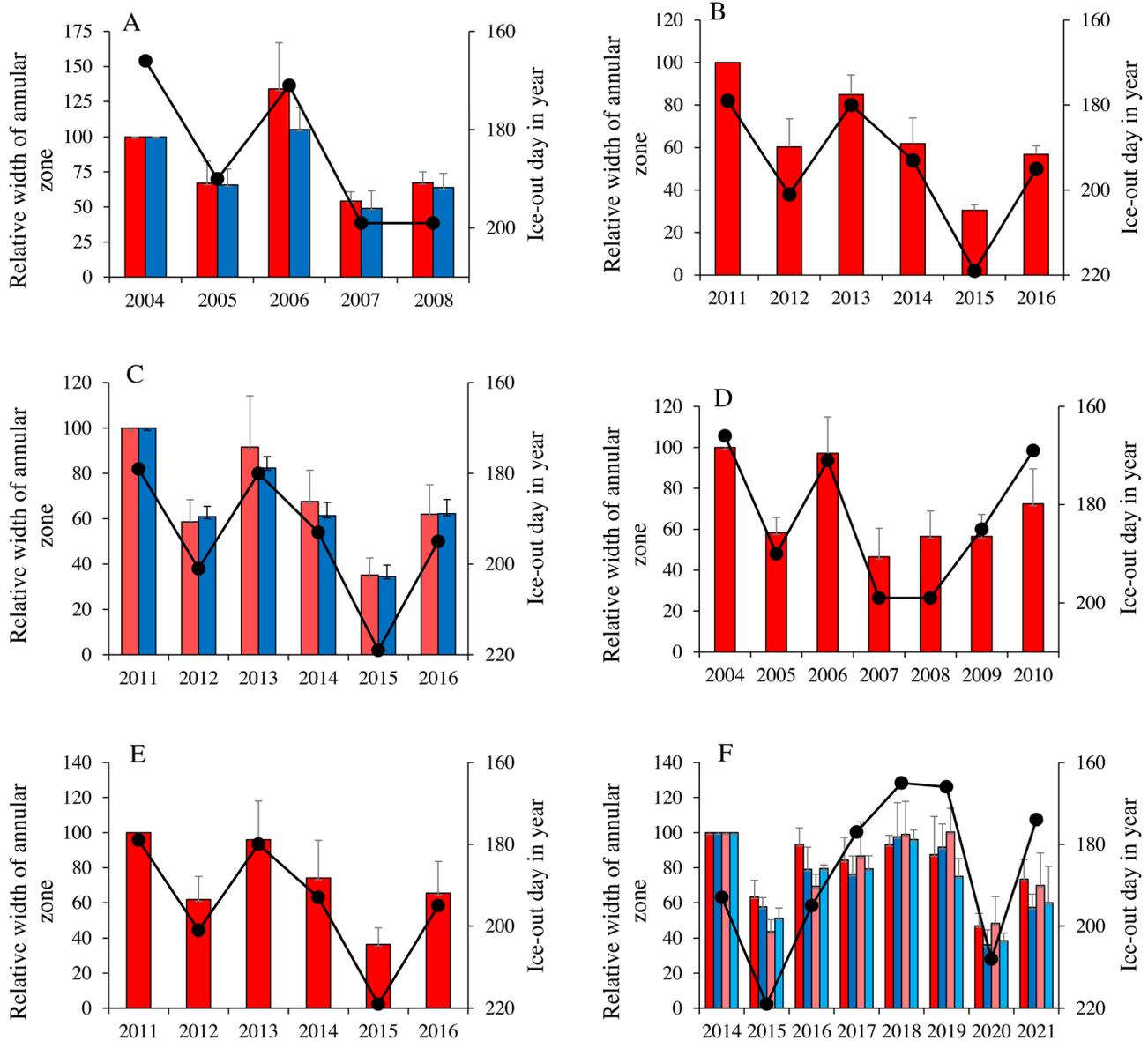


Figure 11. Mean relative width (column) of annular zones in otoliths of brown trout sampled in A) Kollsvatn in 2010-2012, B) Kollsvatn in 2017 and 2018, C) Litlosvatn in 2015, D) Litlosvatn in 2017, and E) Litlosvatn in 2022. The width of the first measured annular zone in each figure (base year) is set to 100. Vertical lines indicate standard deviation of the mean values. The black lines denote ice-out day in year.

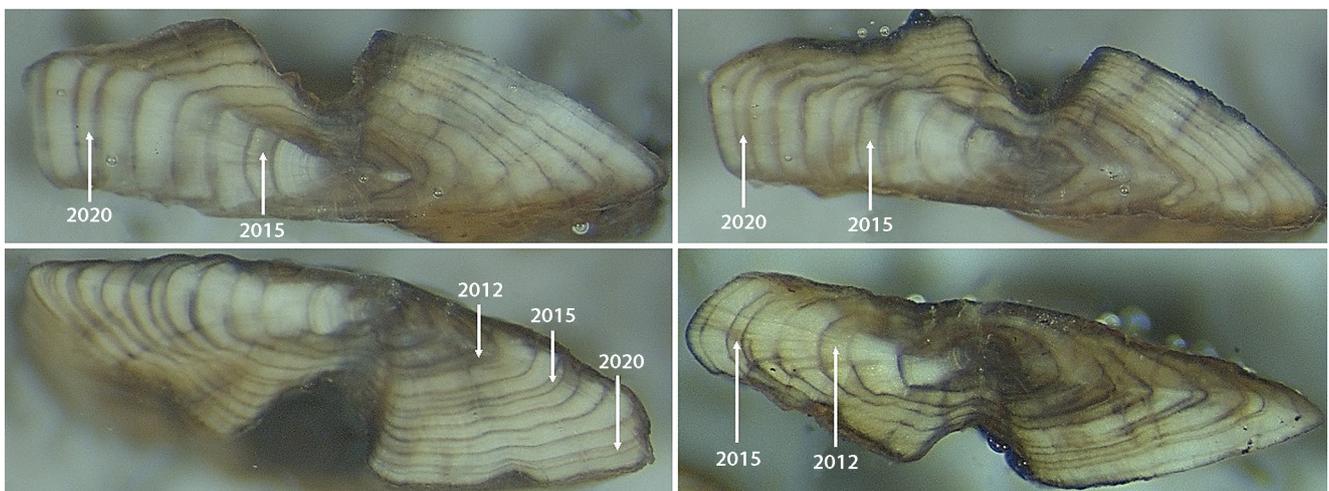


Figure 12. Burnt cross sections of otoliths from brown trout from Litlosvatn (A-C) and Kollsvatn (D). A) individual from year-class 2014, captured in 2022, B) individual from year-class 2012, captured in 2022, C) individual from year-class 2010, captured in 2022, and D) individual from year-class 2010, captured in 2017. The arrows mark the narrow annular zones formed in the years 2012, 2015, and 2020.

given decreasing widths as the fish becomes older. Apparently, delayed ice-offs result in much narrower annular zones than in the subsequent years with early ice-offs. Annual growth rate in brown trout is highly correlated with temperature (Elliott 1976; Lobón-Cerviá *et al.* 1998) and population density (Jensen 1977; Al-Chokhachy *et al.* 2022). Brown trout population density in Litlosvatn and Kollsvatn may vary over time due to variations in annual recruitment and exploitation, but it is unlikely that the synchronous growth variations in the two lakes should be a result of frequent and parallel density shifts. Accordingly, the significant relationship between ice-out day and brown trout growth in the lakes Litlosvatn and Kollsvatn is most probably related to water temperature. In these alpine localities, stream and lake temperature is relatively low even in the warmest summers, and the positive relationship between early ice-out and trout growth fits well with the positive relationships between summer stream temperature and trout body size found by e.g. Al-Chokhachy *et al.* (2022).

Snow cover may not only depress air temperatures (Walsh *et al.* 1985; Mote 2008), but also water temperatures in the streams during the summer, partly due to the remaining snow covering streams, and partly due to cold melt water, as observed during July and August 2003–2021 in Krokavassbekken, one of the inlet streams to Kollsvatn. During summers with much leftover snow, mean stream temperature was considerably depressed, probably contributing to delayed warming of the lakes in such summers as well. Age-class 2–4 years which were included in the growth analyses, may be a mixture of individuals which have stayed both in the streams and in the lakes at these ages. Nevertheless, all individuals express the same growth response, indicating that the temperature regimes in both lotic and lentic habitats may fluctuate in the same manner.

Much snow, delayed ice break-ups, and low water temperatures during summer may not only have a direct effect on brown trout growth, but also an indirect effect by affecting the food rations and energetic quality of food items ingested by brown trout in high elevation lakes. Hatching and growth of the large phyllopod, *Lepidurus arcticus* (Pallas, 1793), one of the most important brown trout food items on Hardangervidda and other mountain areas in southern Norway (Aass 1969; Rognerud *et al.* 2003; Qvenild *et al.* 2018; Hesthagen & Kleiven 2021) is also influenced by water temperature. In lakes with early ice break-ups, *L. arcticus* may become an important part of brown trout diet already from the end of June and beginning of July (Borgstrøm 1970). In summers with much snow and late ice break-ups, hatching of eggs may be heavily delayed, as was observed in the end of July 1993 when *L. arcticus* had only reached the third instar in Litlosvatn (Borgstrøm 1997). Delayed development of this species in cold summers has also been observed in lower parts of the Kvenna watercourse (Qvenild *et al.* 2018). The small growth increments in the otoliths of brown trout, especially in the years 2012, 2015, and 2020 may accordingly be related to a low water temperature in combination with less availability of important food items such as *L. arcticus*.

Temperature was early identified as a controlling factor in marine fisheries (Rollesfsen 1948), and with a significant positive relationship between recruitment and temperature for species like cod *Gadus morhua* L. 1758, haddock *Melanogrammus aeglefinus* L. 1758 and herring *Clupea harengus* L. 1758 (Bogstad *et al.* 2013). Although at a smaller scale compared to the marine fisheries, the low annual brown trout yield obtained from lakes on Hardangervidda during the 1920s and the first years of the 1930s, followed by a substantial increase in yields during the next years, have been explained by changes in snow depth and summer temperatures (Sunde 1937; Rognerud *et al.* 2003; Qvenild 2004). These environmental conditions influence

not only growth, but also annual recruitment. In the headwater lake, Krokavatn, situated a few kilometers upwards from Kollsvatn, only six strong year-classes appeared during the period 1970–2003 (Borgstrøm & Museth 2005). Recruitment failures depended significantly on the accumulated snow depth in April. In addition, size of young-of-the-year brown trout at onset of the winter seemed to be crucial for their survival. Brown trout have in general a relatively slow annual growth in lakes on Hardangervidda, usually becoming mature at an age of eight years and even older, at lengths in the range 30–40 cm or larger (Sømme 1934; Thaulow *et al.* 2017), i.e., at sizes attractive to fishermen. Thus, frequent years with much accumulated snow, as observed in the period 2001–2022, give a delayed growth to preferred catchable size, as well as a risk for reduced recruitment.

In conclusion, opposite the increasing trend in air temperatures and an earlier date of ice-free lakes both in North America and Europe during the last decades, years with high winter precipitation and more accumulated snow are still frequent in the western mountain range in southern Norway. Since the combined environmental variables spring snow depth and date of ice-free lake highly affect both annual recruitment and growth of brown trout, these variables may be used in forecasts of brown trout yields from lakes in this mountain area.

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