

RECLAIMING AUTUMN IN LIMNOLOGY: EVIDENCE OF SHIFTING AUTUMN
PHENOLOGY AND IMPACTS ON WINTER CONDITIONS AND CROSS-SEASONAL
LAKE DYNAMICS

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Abstract

Autumn remains understudied in limnology, despite its recognized ecological importance in other disciplines. In this thesis, we addressed the need for greater integration of autumn into limnological research (Chapter 1) and demonstrated how climate-driven shifts in autumn phenology affect ice formation and winter thermal conditions (Chapter 2). Using 37–50 years of data from 47 Finnish lakes, we found that autumn surface waters have warmed significantly, resulting in widespread delays in ice formation. Delayed ice formation was associated with colder bottom under-ice temperatures. Stronger autumn winds and larger lake size were also associated with colder under-ice conditions through their influence on pre-freeze mixing and heat loss. Furthermore, higher maximum summer surface water temperatures were observed in years with later ice-on dates. As climate change continues to disrupt seasonal patterns, a greater focus on autumn will be critical to effectively predict the impacts of warming on ecosystem functioning of northern lakes.

Dedication

I dedicate this work to my sweet boy Hopper in the sky.

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Table of contents

Abstract.....	ii
Dedication.....	iii
Acknowledgments.....	iv
Table of Contents.....	vi
List of Figures.....	viii
General introduction	1
References.....	4
Chapter 1: Autumn as an overlooked opportunity for limnology:.....	8
My contribution.....	9
Citation for M.Sc. thesis.....	9
1. Introduction	10
2. The complexity of defining autumn in limnology.....	10
3. The importance of autumn for limnology.....	11
4. Opportunities for future directions.....	13
Acknowledgements	14
References	15
Figure	17
Chapter 2: Phenological shifts in autumn drive changes in ice-on timing and under-ice water temperature in Finnish lakes.....	19
My contribution	20
Citation for M.Sc. thesis.....	20
Abstract	21
1. Introduction	22
Research Questions.....	25
2. Materials and Methods	26
2.1. Data acquisition	26
2.2. Data analysis	28
2.2.1. Defining autumn length.....	28
2.2.2. Trend analysis	28
2.2.3. Anomaly and breakpoint analysis.....	29
2.2.4. Spearman's rank correlations.....	29
2.2.5. Regression tree analysis.....	30
2.2.6. Structural equation model (SEM): Autumn → Winter.....	30

2.2.7. Structural equation model (SEM): cross-seasonal model.....	31
3. Results	32
3.1. How are autumn open-water temperatures, ice-on dates, and under-ice water temperatures changing over time in lakes across Finland.....	32
3.1.1. How are autumn open-water temperatures changing over time in lakes across Finland?.....	32
3.1.2. How are ice-on dates changing over time in lakes across Finland.....	32
3.1.3. How are under-ice water temperatures changing over time in lakes across Finland.....	33
3.2. What are the relationships between autumn conditions, ice-on timing, and bottom under-ice water temperatures?.....	34
3.2.1. What are the drivers of under-ice water temperature?.....	34
3.2.2. How do autumn conditions and lake morphology interact to influence bottom under-ice water temperature, ice phenology, and autumn duration?.....	35
3.3. Do autumn and winter conditions influence subsequent maximum summer surface water temperatures?.....	36
4. Discussion	37
4.1. Autumn warming and delayed ice formation.....	37
4.2. General cooling of under-ice water temperatures	39
4.3. Drivers of under-ice water temperature.....	41
4.4. Cross-seasonal interactions and the influence of summer climate	43
5. Ecological implications	45
6. Conclusion	46
Acknowledgements	47
References	48
Figures	61
Supplementary materials	69
General Conclusion.....	79

List of Figures

Chapter 1:

Figure 1. Four Web of Science searches for titles and abstracts were conducted using the search string (lake* OR reservoir* OR pond) AND season (winter, autumn, spring, or summer) for studies published between 2000 and 2024. Search results for: A) the proportion of total limnological studies published in each year focusing on spring, summer, autumn, and winter, and B) the cumulative number of publications for each season. To illustrate that limnological data collection is uncommon relative to summer and spring, we highlight: C) the number of secchi disk samples collected in the United States by month based on data available in the Water Quality Portal (De La Torre et al. 2025). Together, these results imply that not only is autumn less well studied in the limnological literature, but also publicly available data necessary to synthesize autumnal change are lacking.

Chapter 2:

Figure 1. Flowchart summarizing the analytical framework used to address the study's three primary research questions. The diagram outlines which datasets and subsets of sites that were used for each question, based on data availability, time series consistency, and the statistical test applied.

Figure 2. Long-term trends and relationships among autumn surface water temperature, ice-on date (calculated as day of year), and under-ice bottom water temperature in Finnish lakes.

Monotonic trends were assessed using the Mann-Kendall test with Theil-Sen's slope estimates ($p < 0.05$) for (A) autumn surface water temperature (October 1st to ice-on date) over 50 years, (B) ice-on date over 50 years, and (C) under-ice bottom water temperature over 37 years. Spearman's rank correlations were used to examine relationships between (D) autumn surface water temperature and ice-on date, and (E) ice-on date and under-ice bottom water temperature. Panels d and e include a linear regression fit (black line) and locally weighted smoothing (LOWESS; blue dashed line) with shading indicating associated 95% confidence intervals. Note the different magnitudes within the legend bars in panels A-C.

Figure 3. Long-term anomalies and breakpoints in ice-on date (calculated as day of year) and under-ice bottom water temperatures in Finnish lakes. Anomalies of (A) ice-on date from 1972 to 2021, calculated relative to the 50-year mean of November 26th (i.e., ordinal day 330) and (B) under-ice bottom water temperature from 1985 to 2021, calculated relative to the 37-year mean of 2.58 °C. Time series of (C) ice-on anomalies and (D) under-ice water temperature anomalies, with segmented means before and after identified breakpoints, and associated 95% confidence interval.

Figure 4. Regression tree predicting average bottom under-ice water temperature based on lake morphology, autumn dynamics, and autumn and early winter meteorological variables in 9 sites across Finland. n represents the number of yearly observations in each node, and maps below each terminal node illustrate where individual observations occurred.

Figure 5. Structural equation model illustrating: (A) the relationships between autumn meteorological variables, lake morphology, and autumn seasonal dynamics in predicting average under-ice bottom water temperature, ice-on date (calculated as day of year), and autumn length in 9 sites across Finland. Solid arrows represent hypothesized causal pathways, with standardized path coefficients indicating the strength and direction of relationships. Double-headed arrows indicate covariance between variables, while dashed, double-headed arrows represent covariance relationships added by the model. Non-significant paths are shown in grey. From the structural equation modeling data, Spearman's rank correlations are displayed for four selected relationships, including (B) autumn length and ice-on date, (C) autumn length and under-ice bottom water temperatures, (D) ice-on date and under-ice bottom water temperatures, and (E) wind speed and under-ice bottom water temperature to illustrate both total and indirect effects. Black lines represent linear fits, while the grey shading indicates the 95% confidence interval. Dashed regression lines are shown for relationships modeled solely as covariances in the structural equation model. Model fit: RMSEA: 0.044, SRMR: 0.029, CFI: 0.997, TLI: 0.992, χ^2 : 0.162

Figure 6. Structural equation model illustrating (A) the cross-seasonal relationships between autumn and winter water temperatures, ice phenology, and summer maximum surface water temperature in 5 lakes across Finland. Ice-on and ice-off dates were numerically expressed as day of year for analyses. Solid arrows represent hypothesized causal pathways, with standardized path coefficients that indicate the strength and direction of relationships. Non-significant relationships are shown in grey. From the structural equation modeling data, Spearman's rank correlations are displayed for three selected relationships, including (B) ice-off date and maximum summer surface water temperature, (C) ice-on date and ice-off date, and (D) ice-on date and maximum summer surface water temperature. Black lines represent linear fits and grey shading indicates 95% confidence intervals. Model fit: SRMR: 0.043, CFI: 0.99, TLI: 0.96, χ^2 : 0.053.

General introduction

Lakes are dynamic sentinels of climate change, responding rapidly to shifts in temperature and seasonality (Adrian et al., 2009). Though lakes occupy only a small fraction of the Earth's surface (USGS, 2019), lakes play a disproportionately important role in global biogeochemical cycles, biodiversity, and regional climate regulation (ACIA 2004; Rosenzweig et al. 2007; Williamson et al., 2009). The sensitivity of lakes to climate change is rooted in their strong thermal coupling with the atmosphere, which allows long-term shifts in air temperature to be reflected in the lakes thermal structure and stratification patterns (Livingstone, 2003). These thermal changes ultimately alter ecosystem function, making lakes critical indicators of ecological change in freshwater systems worldwide (Adrian et al., 2009; Williamson et al., 2009).

Climate change is driving measurable physical changes across lakes worldwide. Rising air temperatures have altered the timing and duration of seasonal lake processes, including earlier spring ice break-up (Šmejkalová et al., 2016), stronger and longer summer stratification (Woolway et al., 2021), and shorter periods of ice cover (Sharma et al., 2021). These physical changes have been linked to cascading ecological effects such as deep water oxygen depletion (Foley et al., 2012; Ficker et al., 2017; Jane et al., 2021; Jansen et al., 2024), altered phytoplankton productivity (Maier et al., 2019; Adams et al., 2022; Dory et al., 2024), and disrupted nutrient cycling (Denfeld et al., 2018; Julian et al., 2025). However, much of limnological research has traditionally focused on the open-water season, particularly spring and summer, when biological productivity is highest and sampling is most accessible. Sampling efforts tend to decline sharply after summer (De La Torre et al., 2025), leaving autumn comparatively underexplored. This seasonal bias has created a critical gap in our understanding

of how climate change affects year-round lake dynamics, particularly in how transitional periods like autumn mediate physical and ecological processes across seasons.

Autumn is a pivotal period in lake ecosystems, serving as a bridge between summer stratification and winter ice cover. During this time, lakes undergo rapid thermal and ecological transitions, including the breakdown of stratification (Boehrer and Schultze, 2008), redistribution of nutrients (Niemistö and Horppila, 2007; Woolway and Merchant, 2019), and setting thermal conditions that persist beneath the ice (Yang et al., 2021; Olesky and Richardson, 2024). As climate warming delays autumn cooling and alters mixing regimes, the timing and intensity of these processes are shifting (Woolway et al., 2021), with potential consequences for succeeding seasons. For instance, shifts in autumn weather conditions, such as storms, can enhance primary production under ice, highlighting the importance of autumn in shaping subsequent seasonal dynamics (Hampton et al., 2024). Despite its ecological importance, autumn remains one of the least monitored and understood seasons in limnology and is often overlooked in climate change studies (Gallinat et al., 2015).

This thesis addresses this research gap by centering autumn as a key driver of seasonal transitions in lake ecosystems. The first chapter, *Autumn as an Overlooked Opportunity for Limnology*, synthesizes current literature to underscore the physical and ecological significance of autumn in dimictic lakes. We argue that autumn plays a critical role in shaping winter conditions, yet remains underrepresented in limnological research due to its transitional nature and the scarcity of long-term observational data during this period. This chapter provides a basis for understanding how phenological changes in autumn may alter lake responses to ongoing climate warming.

Building on the first chapter, the second chapter examines empirical data on autumn and winter lake processes to assess how autumn dynamics influence ice-on timing and under-ice water temperatures across Finnish lakes. This work addresses the following questions: (1) How are autumn surface water temperatures, ice-on dates, and under-ice water temperatures changing over time in lakes across Finland? (2) What are the relationships between autumn conditions, ice-on timing, and bottom under-ice water temperatures? (3) Do autumn and winter conditions influence subsequent maximum summer surface water temperature? Analysis of these questions advance our understanding of autumn's role in mediating cross-seasonal lake dynamics. These questions will also provide critical insights into key changes in ice phenology and under-ice thermal structure, both of which are crucial to biological activity under the ice. Together, these chapters underscore the ecological importance of autumn, challenging the traditional research focus of spring and summer, and calling for greater attention to the impacts of changing autumns in a warming world.

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Chapter 1:

Autumn as an overlooked opportunity for limnology

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My Contribution

The manuscript *Autumn as an overlooked opportunity for limnology* was published in PLOS Climate. I served as a joint first author together with Sapna Sharma. I led the manuscript writing and editing, and co-wrote the original draft with Sapna Sharma and Joshua Culpepper. The project was conceptualized by Faith Ferrato, Sapna Sharma, Joshua Culpepper, Ceara Talbot, Michael Meyer, and Stephanie Hampton. Formal analysis was completed by Ceara Talbot and Michael Meyer. Revisions and review were completed by Faith Ferrato, Sapna Sharma, Joshua Culpepper, Ceara Talbot, Michael Meyer, and Stephanie Hampton.

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1. Introduction

Ecological disciplines, from forestry to soil sciences and ornithology, recognize the critical role of autumn in an array of physical and biological processes. Terrestrial studies categorize autumn as the end of the growing season. Autumn weather conditions can disrupt plant-soil interactions, affecting nutrient cycling and soil fertility (Broadbent et al., 2024); determine dormancy and freezing tolerance of trees during winter (Chang et al., 2016); and create phenological mismatches that affect diet quality and predator-prey relationships (Gallinat et al., 2015). In many lakes, autumn is marked by an important period of flux within the water column, affecting nutrient cycling, phytoplankton, and fish productivity (Winder and Sommer, 2012). Despite its importance, autumnal limnological processes remain understudied.

2. The complexity of defining autumn in limnology

In part, autumn research in limnology is hindered by the lack of consistency amongst definitions, which complicates direct comparisons among studies and may not capture key limnological conditions. Autumn definitions primarily fall into two categories: astronomical seasons and meteorological forcing. Astronomically, autumn begins at the autumn equinox and ends at the winter solstice. A meteorological focus on autumn is defined as the period between September 1st to November 30th in the Northern Hemisphere and March 1st to May 31st in the Southern Hemisphere (NOAA, 2016). This standardization ensures comparability across studies, particularly for climate analysis (NOAA, 2016). However, within limnology, the interest in autumn lies in the change in a lake's thermal structure from stable stratification to a period of turnover prior to winter ice cover, which is not always appropriately captured by astronomical or meteorological definitions.

Limnological definitions of autumn vary from single-day to multi-day events. Definitions that include single-day events, such as the onset of an isotherm (e.g., consistent temperature throughout the water column, specifically the date surface-to-bottom water temperature differences are less than 2°C) (Magee et al., 2016), provide a clear and quantifiable event that allows for direct interannual comparisons and trend analyses over time. However, these definitions treat autumn as a single point, which does not facilitate the understanding of the gradual nature of autumn as a period. In contrast, multiday definitions (e.g., the duration from breakdown of stratification to ice formation) in lakes capture the entire transition, offering a more ecologically relevant period for assessing lake ecosystem changes (Oleksy and Richardson, 2024). Defining autumn with a beginning and end more accurately reflects ecological phenomena (e.g., leaf senescence) (Gallinat et al., 2015), and introduces variability, as the duration of this period may change significantly between years and locations. The challenge limnologists face is to identify which definition is the most relevant for a given study and which definition permits comparisons across individual studies. For example, do we favor a simple definition that remains consistent through time or a complex and data-intensive definition that targets a specific ecosystem of interest?

3. The importance of autumn for limnology

Despite being a critical transitional period, autumn has historically been less well represented in the published literature and sampling events (Figure 1). We conducted a structured literature survey in Web of Science to assess the number of seasonal limnological studies published between 2000 and 2024. Annually, a maximum of 10% of limnological studies investigated focus on autumn (Figure 1a), and this rate has only marginally increased since 2000

(Figure 1b). Furthermore, publicly available limnological data shows diminished sampling following spring and summer, implying limited capacity to synthesize existing autumnal data (De La Torre et al., 2025) (e.g., secchi depth; Figure 1c). Among all seasons, summer dominates research, likely because peak biological productivity occurs in summer. Consequently, researchers often prioritize spring monitoring to anticipate summer conditions, after which sampling effort substantially declines. Similar levels of attention have not yet been paid to autumn as a critical transition season. Unlike spring, which often has sudden and apparent changes (e.g., ice breakup and spring leafout), autumn is characterized by gradual shifts in phenology, increasing the difficulty to identify key events (Gallinat et al., 2015).

The study of autumn is becoming increasingly important as global environmental changes accelerate. Climate change contributes to shorter winters, longer summers, stronger and longer periods of stratification during the open-water season, and altered mixing regimes (Woolway et al., 2020). While autumn climate may not be changing as rapidly as other seasons (Wang et al., 2021), subtle variations in autumn climate result in measurable shifts in autumn limnological conditions. Furthermore, autumn climate plays a critical role in winter conditions such as the timing of ice formation (Hewitt et al., 2018) and strong autumn storms can enhance primary production and increase chlorophyll concentrations under the ice (Hampton et al., 2024), highlighting the importance of autumn conditions to under-ice ecological processes. Biological communities may also be impacted by seasonal changes because zooplankton rely on autumn feeding for winter survival, and the resuspension of dormant stages during this period can shape seasonal population dynamics (Jewson, 1992). A greater emphasis on investigating autumnal processes would highlight how lake ecosystems are shaped in autumn and how long-term changes may influence cross-seasonal dynamics.

4. Opportunities for future directions

Cross-seasonal interactions shape ecosystem function, yet the role of transitional seasons (i.e., spring and autumn) remains poorly understood. Future research in limnology could address these gaps by placing greater emphasis on interseasonal dynamics to recognize autumn as a critical, but understudied, component of ecological memory. Given that ecosystem functions progress over extended periods rather than discrete moments (Palmer and Febria, 2012), understanding how autumn dynamics shape winter conditions and carry over to subsequent seasons is essential for capturing the full complexity of ecosystem processes. Establishing reference points and baseline conditions for autumn is essential to understanding long-term changes because future shifts may be more pronounced than contemporary observations. Moreover, establishing a baseline requires typifying features of autumns across a range of biomes. While understanding of autumnal limnology is already limited in otherwise well-studied northern temperate regions (Williams, 1988), understanding of limnological autumn dynamics is likely even more limited in tropical and non-freezing lakes. In these regions, seasonal transitions differ fundamentally from those in temperate systems, thereby restricting the ability to generalize seasonal patterns across different lake types. At present, the lack of autumn research leaves significant knowledge gaps that limit the ability to understand year-round limnological dynamics and predict future ecosystem changes. Addressing these gaps would ultimately enhance the ability to assess how lakes will respond to global environmental change.

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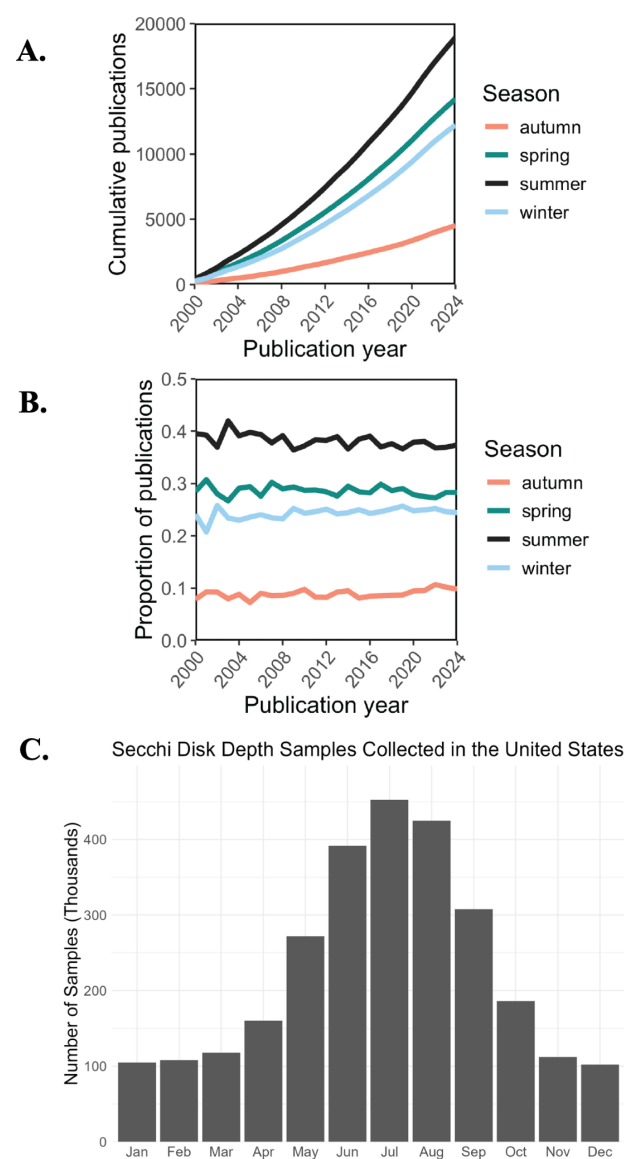
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Figure 1. Four Web of Science searches for titles and abstracts were conducted using the search string (lake* OR reservoir* OR pond) AND season (winter, autumn, spring, or summer) for studies published between 2000 and 2024. Search results for: A) the proportion of total limnological studies published in each year focusing on spring, summer, autumn, and winter, and

B) the cumulative number of publications for each season. To illustrate that limnological data collection is uncommon relative to summer and spring, we highlight: C) the number of secchi disk samples collected in the United States by month based on data available in the Water Quality Portal (De La Torre et al. 2025). Together, these results imply that not only is autumn less well studied in the limnological literature, but also publicly available data necessary to synthesize autumnal change are lacking.

Chapter 2:

Phenological shifts in autumn drive changes in ice-on timing and under-ice water
temperature in Finnish lakes

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My contribution

The manuscript *Phenological shifts in autumn drive changes in ice-on timing and under-ice water temperature in Finnish lakes* was submitted to Water Resources Research. The project was conceptualized by Faith Ferrato and Sapna Sharma. Formal analysis was completed by Faith Ferrato. The original draft was written by Faith Ferrato. Revisions and reviews were completed by Faith Ferrato, Sapna Sharma, Joshua Culpepper, Merja Pulkkanen, and Raine Kortet.

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Abstract

Autumn is a pivotal but understudied season in limnology. As climate change alters the timing and duration of autumnal cooling, the implications for winter thermal structure and long-term ecosystem function in dimictic lakes remain uncertain. To address this gap, we synthesized 37–50 years of data from 47 Finnish lake sites, providing the first comprehensive long-term assessment of how autumn conditions indirectly govern winter thermal regimes. Furthermore, we examined how autumn surface warming, winter under-ice temperatures, and ice phenology influence maximum summer surface water temperature. We found that autumn surface waters warmed by 0.37°C per decade, delaying ice-on by 4.1 days per decade over the last 50 years. Interestingly, later ice formation correlated with colder under-ice bottom water temperatures ($r = -0.54$), with a marked regime shift in 2002 toward later freezing and cooler bottom water conditions. Additionally, our structural equation model linked stronger autumn winds, higher autumn shortwave radiation, and lakes with larger areas to colder under-ice water temperatures, likely due to their influence on lake water cooling and ice formation. Furthermore, later ice-on and earlier ice-off led to higher maximum summer surface water temperature; however, under-ice water temperature had no direct effect. As climate warming prolongs autumn and delays ice-on, extended water column mixing and atmospheric exposure can cool under-ice water temperatures. These shifts have potential consequences for oxygen and nutrient dynamics, winter habitat quality, and overall ecosystem resilience, emphasizing the need to integrate autumn dynamics into future limnological research and lake monitoring efforts.

1. Introduction

Autumn plays a critical role in regulating ecosystem processes, as declining temperatures and shorter day lengths trigger changes in productivity, nutrient cycling, and species behavior. For example, prolonged autumn weather conditions can extend the growing season, increasing photosynthetic activity and altering carbon cycling patterns within boreal and temperate forests (Piao et al., 2008; Richardson et al., 2010). Shifts in the timing of autumn can also disrupt bird migration patterns, creating challenges for hunting activities and conservation efforts (Frei et al., 2024). In aquatic systems, autumn weather conditions mediate lake stratification dynamics through evaporative cooling and vertical mixing (Farmer and Carmack, 1981), which can directly impact ice formation and under-ice thermal structure (Yang et al., 2021; Oleksy and Richardson, 2024). Despite the importance of autumn in ecosystem regulation, the impact of shifting autumn phenology remains overlooked in limnology. Autumn has represented a maximum of 10% of limnological studies annually since 2000, with this proportion remaining consistent over the last two decades, leaving a critical knowledge gap of this important transitional period (Ferrato et al., 2025). Understanding the effect of warming autumn conditions is essential to predict broader ecosystem responses to climate change and to increase our understanding of ice-on timing and under-ice processes that have cascading impacts on biological activity in aquatic ecosystems.

Global air temperatures continue to rise at an unprecedented pace, with 2024 recorded as the warmest year since records began in 1850, surpassing the previous record set the prior year (NOAA, 2025). Rising air temperatures have significantly increased global lake surface water temperatures (Schmid et al., 2014; O'Reilly et al., 2015), altering lake thermal structure and mixing regimes (Woolway et al., 2020). While autumn climate is not changing as rapidly as other

seasons (EPA, 2024), shifts to autumn conditions remain ecologically significant, particularly in the breakdown of stratification. Autumn air temperature regulates heat exchange between the lake surface and the atmosphere, leading to density changes that induce vertical mixing of the water column (Woolway et al., 2022). Yet, climate change is hindering this seasonal reset. Prolonged summer stratification and mild autumn air temperatures delay autumn mixing and ice-on (Woolway and Merchant, 2019). The observed changes in thermal regimes emphasize the critical need to understand autumn climate processes and their influence on year-round lake thermal dynamics.

Changing thermal regimes in dimictic lakes will have direct consequences for lake water cooling and winter conditions. Ice formation in Northern Hemisphere lakes has been delayed by an average of 11 days per century (Sharma et al., 2021). While autumn air temperature is consistently the strongest predictor of ice formation in dimictic lakes (Hewitt et al., 2018; Smits et al., 2021), it often explains only a portion of the variability in ice-on timing (Smits et al., 2021). Ice formation requires both sustained temperatures below 0°C and sufficient heat loss in the water column, a process that can be influenced by wind; water movement; and lake, landscape, and groundwater characteristics (Newton and Mullan, 2021). The timing of ice formation impacts many winter processes, including oxygen depletion (Flaim et al., 2020), nutrient cycling (Denfeld et al., 2018), phytoplankton productivity (Maier et al., 2019), and under-ice thermal profiles and circulation (Kirillin et al., 2012). Understanding relationships between autumn meteorology and ice formation is critical to predict future lake ice dynamics and subsequent ecosystem processes.

Although the ecological impacts of lake ice cover are well documented, its influence on under-ice thermal regimes remains poorly understood. Ice cover itself has two opposing effects

on lake thermal profiles. Delayed ice cover increases solar radiation to a lake's surface before freeze-up, leading to warmer under-ice conditions (Gerbush et al., 2008). Conversely, extended open water periods in autumn may enhance heat loss from the lake to the atmosphere, cooling the water column before freeze-up (Kirillin et al., 2012; Titze and Austin 2014; Zhong et al., 2016). The net effects depend on which of these contradictory processes dominate during autumn, with studies reporting contrasting findings. In Mohonk Lake, NY, delayed ice formation contributed to colder under-ice water temperatures (Oleksy and Richardson, 2024), whereas a study on mountain lakes found ice-on timing had no effect on early winter under-ice temperatures (Smits et al., 2021). The broader effects of delayed ice formation on under-ice thermal profiles remain inconclusive (Niedrist et al., 2018), with most research limited to single lake systems (Gerbush et al., 2008; Oleksy and Richardson, 2024), restricting our ability to generalize findings. Moreover, limited long-term data have hindered analysis of under-ice thermal trends and their underlying drivers (Oleksy and Richardson, 2024).

The need to better understand autumn's role in shaping winter lake conditions is underscored by the cross-seasonal nature of limnological processes, where past ecological conditions influence future ecosystem states (Palmer and Febria, 2012). The timing and characteristics of ice cover are primary examples, driving significant biological and physical changes throughout the year. For instance, winter ice cover dictated summer surface water warming trends (O'reilly et al., 2015). However, the role of autumn remains poorly understood in cross-seasonal context, despite its importance in shaping winter conditions (Hewitt et al., 2018; Smits et al., 2021) and seasonal population dynamics (Jewson, 1992). Thermal conditions in autumn may have lasting effects that extend beyond the ice-cover season, as shifts in under-ice water temperatures influence vertical mixing (Bruesewitz et al., 2015) and nutrient redistribution

into spring (Moss, 2012; Twiss et al., 2012). Understanding the cross-seasonal linkages between autumn, winter, and summer water temperatures are essential to contextualize ecological outcomes.

Finland, where annual air temperatures have risen faster than the global average since 2000 (IEA, 2022), offers important context for studying climate-driven changes in lakes. Finnish lakes have experienced some of the fastest rates of ice loss globally, exceeding those observed in North America and Russia since 1992 (Sharma et al., 2021). Utilizing Finland's exceptionally long-term records of ice phenology and water temperature, we provide the first comprehensive assessment of how shifting autumn conditions have influenced the timing of ice formation and under-ice water temperatures in dimictic lakes over the past 37–50 years. Furthermore, we investigated evidence of cross-seasonal linkages between autumn, winter, and summer water temperatures. We asked: (1) How are autumn surface water temperatures, ice-on dates, and under-ice water temperatures changing over time in lake sites across Finland? (2) What are the relationships between autumn conditions, ice-on timing, and under-ice bottom water temperatures? (3) Do autumn and winter conditions influence subsequent maximum summer surface water temperatures?

As climate change prolongs summer stratification (Woolway and Merchant 2019) and accelerates ice loss (Imrit and Sharma, 2021), many lakes will continue to experience longer autumn periods before freezing (Woolway, 2023). We predict that warmer autumn air temperatures and increased shortwave radiation will elevate autumn surface water temperatures and delay ice formation in lakes across Finland. Prolonged open water periods in autumn increase atmospheric exposure to the lakes surface, allowing for extended wind-driven mixing and heat loss from the water column prior to ice-on. As a result, we hypothesize that lakes will

cool more intensively in late autumn, leading to colder under-ice water temperatures over winter. Additionally, if colder under-ice temperatures persist, we propose that there may be cross-seasonal linkages influencing maximum summer surface water temperatures, potentially creating a negative feedback loop. Identifying how autumn climate conditions influence lake cooling provides insight into variations in ice-on timing and under-ice thermal dynamics, both of which are crucial to biological activity under the ice. Understanding these relationships will be essential for bridging the gap between under-ice and open-water seasons (Salonen et al., 2009) and highlighting the impacts of changing ice phenology on lake ecosystems.

2. Methods

2.1. Data acquisition

Ice-on and ice-off data were obtained from the Finnish Environmental Institute (Syke: open Hertta database) for 47 morphologically diverse lakes from southern to northern Finland from 1972 to 2021. For this dataset, ice-on is defined as the first date that a lake is completely covered with ice and lasts the duration of the winter. Ice-off is defined as the date when ice cover completely melts from the lake surface. In instances when these primary dates were unavailable, we used the earliest recorded date of ice cover, and the last recorded date of partial ice melt as substitutes.

Water temperature data were also acquired from Syke. Under-ice water column measurements were recorded in 9 sites across Finland. Approximately bi-weekly temperature readings were taken at each site from 1985 until 2021. Water temperature measurements were taken at discrete depths, beginning at the surface (0m) and continuing at 1-meter intervals down to 20 meters. In lakes deeper than 20m, measurements increased to 2-meter intervals down to

50m. For sites deeper than 50 meters, readings were recorded at 5-meter intervals down to the lakebed. Vertical temperature profiles were obtained using various digital instruments (see Korhonen, 2002), which became widely available following the early 1970s. Among the 9 sites with under-ice water temperature data, one site (*Lake Pesiöjärvi*) had missing ice data, making it challenging to determine the average under-ice water temperature, as ice-on and ice-off dates are needed for accurate calculations. To address missing ice-on and ice-off dates for Lake Pesiöjärvi, we developed a methodology combining satellite imagery, temperature records, and freezing degree day (FDD) calculations (Supplementary Material).

In addition to under-ice water temperature data, daily surface water temperature data (measured 20 cm below the surface) were collected during the open water periods at 14 sites. The time series coverage varied by site, with some records beginning as early as 1972 and others starting as late as 2001. Surface water temperatures were recorded using an array of devices including mercury thermometers, digital thermometers, and automated temperature meters (physical vapor deposition temperature meter) during open water periods (Korhonen, 2002).

We acquired both meteorological and morphological information for the 9 Finnish lakes with under-ice data. We obtained daily air temperature ($^{\circ}\text{C}$), wind speed (m/s), precipitation (mm), snow depth (mm), and downward shortwave radiation (W/m^2) from ERA5-land. We downloaded these data from the open-access database Climate Engine (Huntington et al., 2017). Lake morphological data were taken from the HydroLAKES database, which integrates information generated by radar technology, long-term imagery composites, and topographic maps (Lehner and Messenger, 2016). Key variables used include lake surface area (km^2), shoreline length (km), total volume (m^3), average depth (m), and elevation (m).

2.2. Data analysis

2.2.1. Defining autumn length

We define autumn length as the period that extends from when the 31-day moving average of daily mean air temperature drops below 4°C to the date of ice-on. This definition allows us to approximate the duration between the breakdown of thermal stratification (i.e., isothermal) and the onset of ice cover, a critical cooling period. While the 0°C isotherm is often used to capture broad seasonal shifts (e.g., Higgins et al., 2021), our definition more closely reflects the thermal changes occurring within lakes during autumn. Ultimately, this standardized definition allows us to make comparisons across lakes of varying geographic regions and provides a framework for understanding the duration of lake cooling during autumn.

How are autumn open-water temperatures, ice-on dates, and under-ice water temperatures changing over time in lakes across Finland?

2.2.2. Trend analysis

We quantified long-term trends in autumn surface water temperatures, ice-on date (calculated as day of year), and under-ice bottom water temperatures (Figure 1). We first determined a significant trend using a Mann-Kendall trend test and subsequently quantified the magnitude of the trend using a Theil-Sen's slope. Both tests were conducted with the package 'trend', selected for its robustness and ability to handle non-normal data (Pohlert, 2023; R Core Team, 2025). For autumn surface water temperature, water temperatures were averaged from October 1st until ice-on for 8 sites with a minimum of 50 years of data from 1972 to 2021 (Figure 1). Data gaps within the 50-year period were filled by imputing missing autumn surface water temperatures, using site-specific averages. For ice-on date, we calculated trends for 47

sites with a minimum of 50 years of data from 1972 to 2021 (Figure 1). In instances with missing years, we imputed the site-specific average ice-on date. Under-ice water temperature trends were quantified at 8 sites with a minimum of 37 years of data, from 1985 to 2021 (Figure 1). To identify changes in under-ice bottom water temperature, we averaged the water temperatures at discrete depths above the lakebed throughout the ice cover period. While the discrete depths varied by site (1-15m above the lakebed), we selected the most consistently available depth throughout the time series to ensure comparability across years. Across these 8 sites, samples were taken 8m above the lakebed on average, where mean maximum lake depth was 44m.

2.2.3. Anomaly and breakpoint analysis

To identify significant shifts in ice-on timing and under-ice bottom water temperature, we calculated yearly anomalies by subtracting the long-term mean of ice-on date or bottom water temperature from each year's average. We then conducted breakpoint analyses with package 'strucchange' (Zeileis et al., 2006).

What are the relationships between autumn conditions, ice-on timing, and under-ice bottom water temperatures?

2.2.4. Spearman's rank correlations

To assess fundamental relationships between key limnological variables, we conducted Spearman's rank correlation analyses. This non-parametric method evaluates monotonic associations while avoiding assumptions about data distribution, making it particularly suitable for ecological datasets (Zar, 2005). Our analysis focused on two critical pairwise relationships: (1) autumn surface water temperatures and ice-on date and (2) ice-on date and under-ice bottom water temperature. The datasets used in each analysis varied based on complete paired

observations of both variables (see Figure 1). These simple correlations serve as an important first step in identifying fundamental relationships within these lake systems.

2.2.5. Regression tree analysis

To identify key drivers of under-ice bottom water temperature, we conducted a regression tree analysis using the ‘rpart’ package (Therneau and Atkinson, 2022) across 9 sites in Finland (Figure 1). Regression tree analysis is particularly suited for ecological datasets because it accommodates non-linear relationships and interactions among predictors (De'ath and Fabricius, 2000). Predictor variables included lake geographic position (latitude), morphological characteristics (lake area, shoreline length, lake volume, lake depth, elevation), climate metrics (air temperature, wind speed, precipitation, snow depth, and shortwave radiation) and autumn seasonal metrics (autumn length). Climate metrics were calculated for autumn (October-December), 2 weeks before ice-on, 1 month before ice-on, and December. These different temporal windows were selected to evaluate which period most strongly influences pre-freeze lake cooling and under-ice thermal conditions, and to account for variability in ice-on timing among lakes. For predictor variables that were skewed, variables were log transformed, as regression trees perform better with symmetrically distributed data (Galili and Meilijson, 2016). This allowed us to assess how under-ice bottom water temperatures are related to several autumn, early winter, and morphological predictor variables, helping to identify key factors that contribute to under-ice conditions.

2.2.6. Structural equation model: Autumn → Winter

Although empirical statistical approaches provide valuable insights into broad environmental relationships between limnological variables, they may oversimplify associations and do not account for confounding factors or directional relationships. Structural equation

modeling overcomes these limitations by quantifying both direct and indirect causal pathways, making it beneficial to understand complex ecological networks. Using the ‘lavan’ package (Rosseel, 2012), we created a model linking autumn climatic variables (October-December), ice-on date, and average under-ice bottom water temperatures across 9 sites in Finland (Figure 1). This model addressed how autumn climatic drivers and ice phenology influence the winter thermal structure of lakes. We assessed model fit using 5 established metrics: Chi-square (χ^2) test, Comparative Fit Index (CFI), Tucker-Lewis Index (TLI), Root Mean Square Error of Approximation (RMSEA), and Standardized Root Mean Square Error Residual (SRMR). The χ^2 ($p>0.05$) test assesses the absolute fit of the model (Schermerle-Engel et al., 2003), whereas the CFI and TLI (>0.95) evaluate model improvement relative to the null baseline (Hu and Bentler, 1999). RMSEA (<0.06) and SRMR (<0.08) qualify prediction error, where lower values indicate closer alignment between observed and modeled data (Hu and Bentler, 1999). This multi-index approach avoids overreliance on any single metric and provides a robust evaluation of model performance.

Do autumn and winter conditions influence subsequent maximum surface water temperatures in summer?

2.2.7. Structural Equation modeling: Autumn $\rightarrow$ Winter $\rightarrow$ Summer

Lastly, to examine the cross-seasonal effects of autumn and winter processes on summer thermal regimes, we created a secondary structural equation model. This model integrated cross-seasonal data from 5 lakes across Finland with complete paired observations of all variables (Figure 1), incorporating autumn surface water temperatures (October 1st to ice-on), ice phenology, under-ice bottom water temperatures, and maximum summer surface water

temperatures. Model fit was assessed using the same metrics listed above, with the exception of RMSEA. RMSEA can reject well-fitting models when sample sizes and degrees of freedom are low (Kenny et al., 2015). Given that this model included fewer than 200 observations, omitting RMSEA was considered acceptable, provided that all other fit indices indicated a good model fit (Kenny et al., 2015).

3. Results

3.1. How are autumn open-water temperatures, ice-on dates, and under-ice water temperatures changing over time in lakes across Finland?

3.1.1. How has autumn surface water temperature changed over time?

From 1972 to 2021, autumn surface water temperatures warmed at a rate of 0.37°C per decade in 8 sites across Finland, corresponding to a 1.85°C warming in autumn surface water temperatures across the study period (Figure 2a). Of the 8 sites, 7 exhibited statistically significant warming ($p < 0.05$). Over the 50-year period, the warming trends ranged between 0.09°C per decade ($p > 0.05$) and 0.79°C per decade ($p < 0.001$) (Table S1).

3.1.2. How has ice-on date changed over time?

Over the 50-year period (1972-2021), we observed delays in ice-on at a rate of 4.1 days per decade, equivalent to 20 days of ice loss over the study period across all study lakes, with ice loss trends uniform across latitudes (Figure 2b). Pyhäjärvi in Pyhäsalmi showed the most pronounced delay at 8.4 days per decade ($p < 0.001$), while Peerajärvi exhibited the smallest significant trend at 1.5 days per decade ($p < 0.05$). Overall, 81% of locations showed statistically significant changes. In comparison, the recent 25- year period (1997-2021) revealed more rapid rates of ice loss, where southern lakes experienced stronger trends, although not all were

statistically significant (Table S2; Figure S1). Although less pronounced than trends observed in more recent decades, the 50-year period provides evidence of widespread ice loss (Figure 2b).

From 1972 to 2021, the change point detection analysis indicated a breakpoint in ice-on date in 2002 (p-value <0.001). At the breakpoint, on average, ice-on date anomalies shifted to later compared to the 50-year average. Before 2002, ice-on date across the 47 lakes occurred 5.37 days earlier than the long-term mean of ordinal day 330 (approx. November 26th). After the breakpoint, the average ice-on date anomaly was 9.47 days later compared to this baseline (Figure 3a and 3c).

3.1.3. How has under-ice bottom water temperature changed over time?

Under-ice bottom water temperatures exhibited an overall cooling trend from 1985 to 2021, with 6 out of the 8 sites showing negative trends (Figure 2c; Table S3). However, only 3 of the 6 cooling trends were statistically significant ($p < 0.05$), reflecting variability in the strength of trends across lakes. On average across all sites, under-ice bottom water temperatures cooled by 0.07°C per decade, resulting in a total decrease in bottom water temperature of 0.27°C over the 37-year study period. The maximum cooling trend was observed in Lake Konnevesi Näreselkä, at -0.27°C per decade ($p < 0.05$), while Lake Pesiöjärvi exhibited a warming trend, with under-ice bottom water temperatures increasing at 0.32°C per decade ($p < 0.05$). Notably, the 2 warming trends occurred at the highest latitudes ($64-68^{\circ}\text{N}$) (Figure 2c). While the average trend indicates cooling, the significance of individual trends varied, likely due to the length of the time series or lake-specific factors.

The change point detection analysis indicated a breakpoint in under-ice bottom water temperatures in the 2002 ice season (p-value <0.001). At the breakpoint, on average, anomalies shifted to cooler temperatures compared to the 37-year average (2.58°C). The average under-ice

bottom water temperature anomaly for the 8 sites prior to 2002 was 0.14°C warmer than the 1985-2021 mean. After the breakpoint, the average under-ice bottom water temperature anomaly was 0.12°C cooler (Figure 3b and 3d).

3.2. What are the relationships between autumn conditions, ice-on timing, and under-ice bottom water temperatures?

Autumn surface water temperatures and ice-on date were positively correlated ($r = 0.43$, $p < 0.001$), indicating that in years when autumn surface water temperatures were warmer, ice formation was later across these 14 sites (Figure 2d). Moreover, we found a strong negative correlation ($r = -0.55$, $p < 0.001$) between ice-on date and average under-ice bottom water temperature across 9 sites in Finland, indicating that later ice formation is associated with cooler deep under-ice water temperatures (Figure 2e).

3.2.1. What are the drivers of under-ice bottom water temperature?

Regression tree analysis revealed that early winter solar radiation and wind-driven mixing controlled under-ice bottom water temperatures (Figure 4). The initial split in the tree separated lakes based on December shortwave radiation where lower shortwave radiation ($<1.2 \text{ W/m}^2$) resulted in warmer under-ice, bottom-water temperatures over winter (3.4°C). Wind speed was the second-order internal node where autumn wind speeds $>2.5 \text{ m/s}$ resulted in colder under-ice bottom water temperatures (1.7-2.4°C), particularly when coupled with colder December air temperatures ($<-5.8^\circ\text{C}$). In contrast, lakes with wind speeds $<2.5 \text{ m/s}$ showed warmer under-ice bottom water temperatures (2.5-3.4°C), with the warmest conditions occurring when autumn duration was shorter (<28 days). These analyses suggest that higher December

shortwave radiation, stronger autumn winds, and warmer December temperatures contribute to colder under-ice bottom water temperatures. Additionally, lower wind speeds and shorter autumn periods are associated with warmer under-ice conditions. The model explained almost half of the variation in average under-ice bottom water temperatures across these sites (Figure 4; $R^2=0.49$).

3.2.2. How do autumn conditions and lake morphology interact to influence under-ice bottom water temperature, ice phenology, and autumn duration?

Our structural equation model revealed mechanistic pathways through which autumn meteorology and lake morphology govern under-ice water temperatures, ice phenology, and autumn duration (Figure 5). Longer autumn periods were associated with later ice-on dates (coefficient = 0.90, $p < 0.001$), and colder under-ice bottom water temperatures (coefficient = 0.04, $p < 0.001$). Higher minimum temperatures in October, November, and December were related to longer autumn periods and later ice-on dates (coefficient = 0.44, $p < 0.001$; coefficient = 0.72, $p < 0.001$). Higher downward shortwave radiation in October, November, and December were weakly associated with later ice-on dates (coefficient = 0.11, $p < 0.001$). Lake area had no relationship with ice-on date (coefficient = 0.02, $p = 0.21$). Later ice-on dates and larger lakes contributed to cooler under-ice bottom water temperatures (coefficient = -0.42, $p < 0.001$; coefficient = -0.28, $p < 0.001$). Higher wind speeds and shortwave radiation in autumn also contributed to cooler under-ice water temperatures, but had weaker relationships (coefficient = -0.17, $p = 0.007$; coefficient = -0.12, $p = 0.009$). This model explained 46% of the variation in average under-ice bottom water temperature, 61% in ice-on date, and 20% in autumn length.

3.3. Do autumn and winter conditions influence subsequent maximum summer surface water temperatures?

Our secondary structural equation model revealed key pathways through which autumn surface water temperatures, lake ice phenology, and under-ice water temperatures govern maximum summer surface water temperatures (Figure 5). Warmer autumn surface water temperatures were associated with later ice-on dates (coefficient = 0.62, $p < 0.001$). Later ice-on dates were related to cooler under-ice water temperatures and earlier ice-off dates (coefficient = -0.60, $p < 0.001$; coefficient = -0.76, $p < 0.001$). Later ice-on dates (coefficient = 0.34, $p < 0.003$) and later ice-off dates (coefficient = -0.27, $p = 0.01$) were positively correlated with higher maximum surface water temperatures in summer. Under-ice bottom water temperatures showed no significant relationship with maximum summer surface water temperature (coefficient = 0.15, $p < 0.08$). The model fit metrics indicated good overall performance, and the model explained 25% of the variation in maximum summer surface water temperature, 38% in ice-on date, 35% in under-ice water temperature, and 57% in ice-off date.

Although simple relationships between variables seem strong and the model demonstrated acceptable fit (Figure 6), an alternative version of the model was tested to explore the influence of summer climate on winter legacy effects. Specifically, we included a path between mean summer air temperature (June-August) and maximum summer surface water temperature (Figure S2). This addition increased the variance explained in maximum summer surface water temperature by 52 percentage points ($R^2=0.77$), exemplifying the dominant influence of summer air temperature on maximum summer surface water temperature. However, the addition of this variable degraded overall model fit, as indicated by poor performance across standard metrics (Figure S2). This suggests the model's structure became misspecified when the

summer air temperature was included, despite its large explanatory power. Additionally, the paths between winter variables and maximum summer surface water temperature weakened and/or became statistically insignificant.

4. Discussion

Our long-term analyses of dimictic Finnish lakes revealed significant warming of autumn surface water temperatures, delayed ice formation, and cooling of under-ice bottom water temperatures. These observed shifts are causally linked, such that warmer autumn periods prolong autumn duration and heat loss, delaying ice-on and resulting in colder under-ice conditions. By synthesizing multi-decadal ice phenology, surface water temperature, and under-ice depth profile data covering several lakes, this study provides the first comprehensive empirical long-term assessment of how autumn conditions indirectly govern winter thermal regimes, a previously overlooked seasonal linkage. Our findings underscore autumn as a pivotal transitional period, where processes such as wind-driven mixing, solar radiation, and the duration of pre-freeze heat loss collectively shape under-ice water temperatures. These findings ultimately advance our understanding of lake ecosystems by highlighting autumn as a critical driver of winter conditions, with implications for cross-seasonal effects into summer.

4.1. Autumn warming and delayed ice formation

We show that autumn surface water temperatures across Finland have increased significantly since 1972, at an average rate of 0.37°C per decade, surpassing global trends in summer surface water temperatures of 0.34°C per decade (O'Reilly et al., 2015) and comparable with regional summer warming rates observed across Europe (Dokulil et al., 2021, Noori et al., 2023). This warming reflects Finland's heightened sensitivity to climate change due to Arctic

amplification, where high-latitude regions are warming at nearly twice the global average (Post et al., 2019). Between 1979 and 2008, autumn air temperature in Finland rose by over 1.5°C (Tietäväinen et al., 2010), contributing to later ice formation and prolonged open-water periods (Korhonen, 2006). Unlike summer, which is often characterized by thermal stability within temperate lakes, autumn is a period of flux (e.g., turnover and snowmelt inflows). During this time, changes in air temperature directly regulate lake surface heat loss and convective mixing, which are essential for the breakdown of stratification before winter (Shuter et al., 2013). Our findings indicate that warmer autumns may delay this transition by increasing thermal inertia and slowing surface cooling, ultimately delaying this transition and the onset of ice cover (Woolway et al., 2021).

As a result of climate forcing and warming autumn surface water temperatures, ice-on dates in Finnish lakes have been delayed by an average of 4.1 days per decade, well exceeding the Northern Hemisphere average delay of 1.1 days per decade (Sharma et al., 2021). The rapid loss of ice cover in Finland has been documented in previous studies, further illustrating the region's heightened sensitivity to climatic change. In a regional study, Lake Konnevesi exhibited no significant ice loss from 1964 to 1994, but from 1996 to 2020, it experienced a rapid decline of 17 days per decade (Noori et al., 2023). Additionally, among Eurasian lakes spanning four major climate zones, Lake Pääjärvi in Finland showed the most pronounced delay in ice-on at 12.5 days per decade (Zdorovenнова et al., 2025). Together, these trends underscore the importance of understanding regional climate dynamics, as ice loss appears to be occurring at a faster pace in Finland than in many other regions (Sharma et al. 2021). Rapid shifts in ice phenology highlight the need to assess how local climate drivers and lake-specific features contribute to regional variability in ice loss trends.

4.2. General cooling of under-ice water temperatures

We observed a consistent decline in under-ice bottom water temperatures across Finnish lakes from 1985 to 2021, averaging $-0.07\text{ }^{\circ}\text{C}$ per decade despite warming autumn surface water temperatures and later ice-on dates. This counterintuitive trend suggests that longer, milder autumns may promote greater heat loss from the water column before ice-on, resulting in colder under-ice conditions (Saloranta et al., 2009). Our findings show that this cooling was significantly correlated with delayed ice formation ($r = -0.54$), supporting our hypothesis that the timing of ice-on plays a key role in shaping under-ice thermal structure. Longer autumn periods and delayed ice formation also led to colder deep under-ice conditions in Mohonk Lake, New York (Oleksy and Richardson, 2024); however, this relationship is not universally observed. In mountain lakes, surface area and summer water temperatures were the best predictors of early winter thermal conditions (Smits et al., 2021), while in Arctic lakes, under-ice water temperatures depended on lake size, summer heat content, and pre-freeze meteorological conditions (Schwefel et al., 2025). Notably, many of these drivers are linked to ice phenology itself, as they influence a lake's heat budget and the timing of freeze. However, while climate primarily controls ice formation (Palecki and Barry, 1986), lake-specific characteristics modulate how these climate signals affect under-ice thermal conditions. For example, small, sheltered lakes often retain heat and maintain warmer winter temperatures, whereas large, wind-exposed lakes experience colder deep waters under ice (Yang et al., 2021). These patterns demonstrate that ice-on timing, while influential, does not solely dictate under-ice thermal regimes. The effects of ice formation are filtered through regional meteorological forcing and physical lake properties, highlighting the need to include climatic and lake-specific characteristics in predicting winter thermal responses.

We found the strongest under-ice cooling in southern Finnish lakes, which may reflect their heightened sensitivity to recent ice loss. From 1997-2021, southern lakes (60°N-65°N) exhibited greater ice decline than northern lakes (Figure S1), likely driven by air temperature increases in southern Finland (Zdorovenova et al., 2025). Through delayed ice formation, longer open water periods in autumn can promote greater heat loss from the water column before ice-on, resulting in colder under-ice conditions (Oleksy and Richardson, 2024). While the 50-year trends show uniform delays in ice formation, the recent acceleration in ice loss in southern Finland suggests lake warming responses are becoming spatially uneven within the country, with southern lakes experiencing stronger climatic responses. The spatial dependence on lake ice duration has long been recognized, often attributed to latitude as a proxy for air temperature and snowfall patterns (Wynne et al., 1996; Magnuson et al., 1997; Wynne et al., 1998). As a key driver of regional climate, latitude plays an increasingly important role in shaping lake ice phenology under accelerated climate change (Warne et al., 2020). Thus, these results emphasize the importance of geographic context in shaping thermal responses to climate change, and that southern latitudes may be particularly vulnerable to ongoing warming.

A statistically significant breakpoint in 2002 marked a notable shift toward both later ice-on dates and colder under-ice water temperatures, reinforcing the relationship between delayed ice formation and deep-water cooling. This breakpoint may reflect a broader climatic regime shift linked to intensifying atmospheric warming since the early 2000s (IEA, 2022). For example, Finland experienced its most pronounced decadal warming between the 1990s and 2000s (Mikkonen et al., 2015). Between these periods, mean annual air temperatures rose by 0.4°C, the largest increase between consecutive decades since records began in 1840 (Mikkonen et al., 2015). From 2000 to 2020, this warming trend continued, with annual air temperatures in

Finland increasing at a rate significantly higher than the global average (IEA, 2022). The winter of 2002 also featured anomalous weather events, including record-low temperatures in October and the early onset of winter conditions (FMI, 2020). These abrupt climate anomalies may have acted as a catalyst, driving the thermal changes observed in Finnish lakes and disrupting previously stable winter dynamics.

4.3. Drivers of under-ice water temperature

Air temperature and shortwave radiation emerged as critical drivers of under-ice bottom water temperatures, primarily through their influence on ice phenology. Colder bottom water temperatures were consistently associated with higher December shortwave radiation ($>1.2 \text{ W/m}^2$) and warmer December air temperatures ($> -5.8^\circ\text{C}$), likely due to delayed ice formation and prolonged atmospheric exposure (Saloranta et al., 2009). Within our regression tree, lakes with higher shortwave radiation were located at lower latitudes, where ice-on typically occurs later (Warne et al., 2020), partially explaining the stronger cooling signal in these systems (Saloranta et al., 2009). Additionally, both warmer minimum air temperatures and greater shortwave radiation during autumn were directly linked to later ice-on dates in our model, which in turn led to cooler under-ice conditions. However, the overall weak causal effect of autumn shortwave radiation on ice phenology and under-ice temperature suggests that non-radiative heat fluxes, particularly sensible and latent heat exchange, play a dominant role during the autumn transition (Saloranta et al., 2009; Austin, 2024). These fluxes dampen daily temperature fluctuations and reduce the impact of direct solar input on the lake (Saloranta et al., 2009; Austin, 2024).

Colder under-ice bottom water temperatures were consistently observed in lakes experiencing higher autumn wind speeds (>2.5 m/s), suggesting that wind-driven mixing enhances late-season heat loss to the atmosphere. The observed colder bottom water temperatures are likely due to stronger winds disrupting the establishment of stable density gradients, allowing the water column to remain vertically mixed and below the temperature of maximum density (4°C) (Titze and Austin, 2014). As a result, heat continued to be lost from the entire water column, rather than an inversely stratified surface layer. This pattern aligns with the cryomictic model of winter thermal structure, where stronger winds promote convective overturn and cooling of deep water layers prior to ice formation (Yang et al., 2021). However, our model showed a weaker direct effect of wind speed on under-ice bottom water temperatures, likely because wind's efficiency as a mixing agent depends on lake-specific factors (e.g., fetch, stratification depth, and bathymetry; Kirillin et al., 2012), which are partially accounted for in the model's other pathways, such as lake area. Together, these results highlight that stronger winds amplify cooling, whereas calmer conditions prolong heat retention in these systems.

Lake morphology, particularly surface area, significantly influenced under-ice temperatures within our model, with larger lakes generally showing colder under-ice bottom waters. We attribute this to the tendency of larger lakes to freeze later, allowing for prolonged heat loss and deeper convective cooling before ice-on (Saloranta et al., 2009; Yang et al., 2021). However, our analysis did not detect a direct causal relationship between lake area and ice-on timing, contrary to prior studies (L'Abée-Lund et al. 2021). We suggest that the absence of a direct relationship may be due to an indirect effect, driven by the strong correlation between lake area and wind speed within our model. Lakes with larger surface areas have longer fetches, which enhances surface mixing and promotes cooling (Fee et al., 1996). This interpretation

aligns with findings from North American lakes, where larger surface areas facilitate more effective convective heat loss (Woolway et al., 2021). The regression tree did not highlight morphology as a primary predictor of under-ice bottom water temperature, suggesting that meteorological factors dominate thermal dynamics in Finnish lakes (Palecki and Barry, 1986). However, the inclusion of lake area in the structural equation model emphasizes that lake-specific traits can modulate how lakes respond to climate forcing, an important consideration for future projections (Walsh et al., 1998).

Autumn duration was also a key mediator of under-ice cooling. Colder under-ice bottom water temperatures were consistently observed in lakes with autumn periods longer than 28 days. Additionally, extended autumn periods within our model were linked to lower under-ice temperatures. However, this relationship was weaker within our model. The weak relationship suggests that, while autumn duration contributes to under-ice cooling, its influence is linked to the timing of ice formation. In this way, autumn duration serves a dual role. It acts as a mechanism for cooling through extended atmospheric exposure and as a proxy for delayed ice-on (Oleksy and Richardson, 2024), which ultimately governs the onset of thermal stability beneath the ice within these systems (Kirillin et al., 2012).

4.4. Cross-seasonal interactions and the influence of summer climate

Our cross-seasonal model revealed that later ice-on dates were associated with earlier ice-off and higher maximum summer surface water temperatures. This relationship likely reflects a combination of physical mechanisms. First, shorter ice durations extend the period during which lakes can absorb incoming solar radiation, amplifying warming through enhanced heat absorption and a positive ice-albedo feedback (Austin and Colman, 2007, 2008). Second, warmer

winter conditions shorten the period available for ice growth, often resulting in thinner ice that is vulnerable to early spring melt (Ashton, 2011). Thinner ice sheets can also result from insulating snow accumulation shortly after freeze, which limits heat loss and further suppresses bottom ice growth (Leppäranta, 2015; Yang et al., 2012). While our model did not include snow depth or ice thickness, these factors likely contribute to this observed pattern and represent important avenues for future research. Together these mechanisms suggest that later ice-on dates may contribute to both longer-open water periods and thinner ice cover, facilitating greater heat absorption and higher maximum summer surface water temperatures. These interactions reflect a form of ecological memory, where the seasonal timing of one event (e.g., ice-on) influences conditions in subsequent seasons (Peterson, 2002).

While ice phenology is seen to mediate cross-seasonal dynamics in our model, under-ice bottom water temperatures did not significantly influence maximum summer surface water temperatures, suggesting that winter thermal legacies are diluted by spring mix and summer warming. Once stratification begins, the epilimnion rapidly decouples from deeper waters, as ambient air temperatures drive heat accumulation in surface waters (Magee et al., 2016; Winslow et al., 2017). The strong coupling between surface water and air temperature during this period aligns with findings from Lewis and Carey (2024), who demonstrated that summer surface water temperatures are more strongly tied to concurrent air temperatures than to antecedent seasonal conditions. Similarly, Dugan (2021) found that summer epilimnion temperatures in dimictic lakes showed little dependence on ice-off timing, as spring mixing and stratification effectively erase the ecological memory of winter conditions. Instead, summer surface water temperature was primarily governed by summer air temperatures, a pattern further supported by our supplementary structural equation model when average summer air temperature was included as

a predictor (Figure S2). Notably, the addition of summer air temperature weakened or negated the effects of winter conditions (e.g., ice-on and ice-off) on maximum summer surface water temperature, reinforcing the dominant role of summer atmospheric forcing in driving epilimnetic warming (Dugan, 2021). Thus, while our primary model suggests that ice phenology indirectly influences maximum summer surface water temperature by extending the open-water season, supplementary analyses indicate that these cross-seasonal effects may be secondary to or even overridden by the dominant role of summer climate and seasonal heating dynamics.

5. Ecological implications

Shifting autumn phenology has far-reaching consequences for winter lake dynamics and the broader seasonal trajectory of aquatic ecosystems. Changes in the timing and duration of autumn mixing can delay ice formation (Woolway and Merchant 2019), reshape thermal profiles (Yang et al., 2021; Olesky and Richardson, 2024), and redistribute oxygen and nutrients throughout the water column prior to ice cover (Hampton et al., 2017; Flaim et al., 2020), thereby setting the physical and chemical stage for winter conditions. Extended open-water periods prolong light availability and primary production, increasing energy reserves for overwintering consumers and potentially altering spring community dynamics (Hébert et al., 2021). Additionally, prolonged autumn mixing and enhanced heat loss can lead to colder, weakly stratified water columns, disrupting habitat partitioning for overwintering fish (Yang et al., 2021). Warm-adapted species such as European Perch (*Perca fluviatilis*), which depend on stable 4°C benthic refugia to maintain their overwintering metabolism (Ning et al., 2025), may experience energetic stress when bottom temperatures fall below their optimal range. In contrast, species such as Arctic char (*Salvelinus alpinus*), which tolerate near-freezing conditions (Klemetsen et al., 2003; Mulder et al., 2018), could expand their winter foraging niche into

deeper waters, potentially restructuring food webs through altered species interactions and resource competition (Yang et al., 2021). As stratification weakens under ice, vertical mixing may continue during winter, enhancing oxygen availability for benthic invertebrates (Bruesewitz et al., 2015) and redistributing nutrients that fuel phytoplankton productivity in spring (Moss, 2012; Twiss et al., 2012). These feedbacks highlight autumn's role in modifying both habitat structure and ecological interactions within the water column. Recognizing autumn as an active and critical driver of under-ice conditions and cross-seasonal interactions is crucial. Future research should investigate how evolving autumn conditions shape winter habitats and influence biological activity into spring. As climate variability intensifies, integrating autumn into our understanding of seasonal dynamics will be key to predicting the future of lake ecosystems.

6. Conclusion

This study establishes that shifts in autumn phenology reshape under-ice thermal regimes in Finnish lakes through delayed ice formation and enhanced heat loss. We illustrate the unintuitive influence that longer autumns have on lakes, where warmer autumns amplify heat dissipation, leading to deeper cooling that can have cascading effects throughout the aquatic ecosystem. These physical changes alter habitat suitability (Yang et al., 2021), nutrient cycling (Bruesewitz et al., 2015), and phytoplankton communities (Moss, 2012; Twiss et al., 2012), with legacies that persist into spring. Like the documented impacts of autumn on terrestrial ecosystems (Gallinat et al., 2015), our findings underscore autumn as a critical regulator of aquatic processes. Given its influence on both ice-on timing and subsequent under-ice dynamics and seasonal ecological trajectories, autumn should no longer be viewed as a passive transition between summer and winter. Instead, it must be recognized as a critical driver of cross-seasonal interactions in aquatic ecosystems. As climate change continues to disrupt seasonal patterns, a

greater focus on autumn will be essential for predicting the future of northern lakes and the ecosystems they support.

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Figures

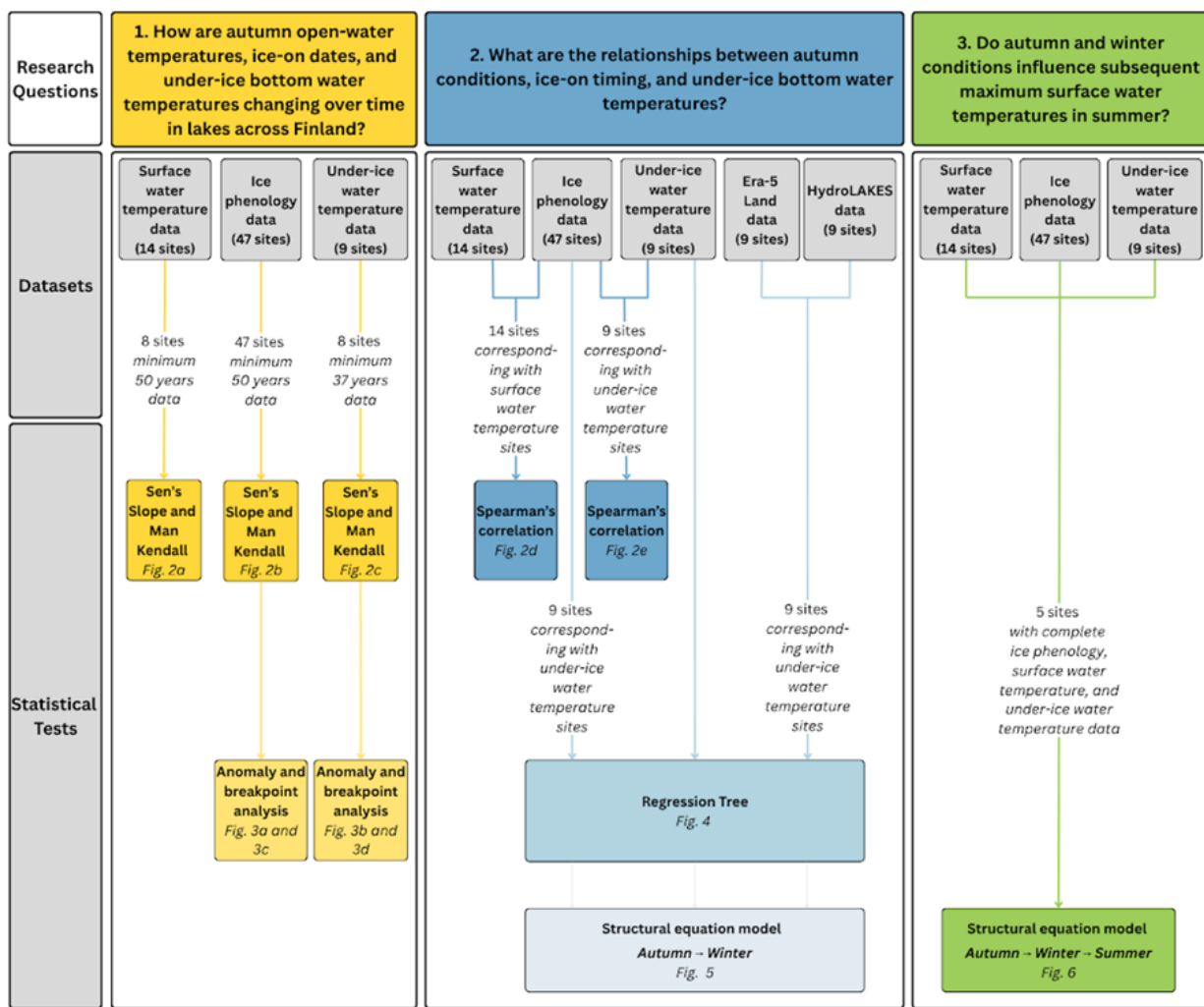


Figure 1. Flowchart summarizing the analytical framework used to address the study's three primary research questions. The diagram outlines which datasets and subsets of sites that were used for each question, based on data availability, time series consistency, and the statistical test applied.

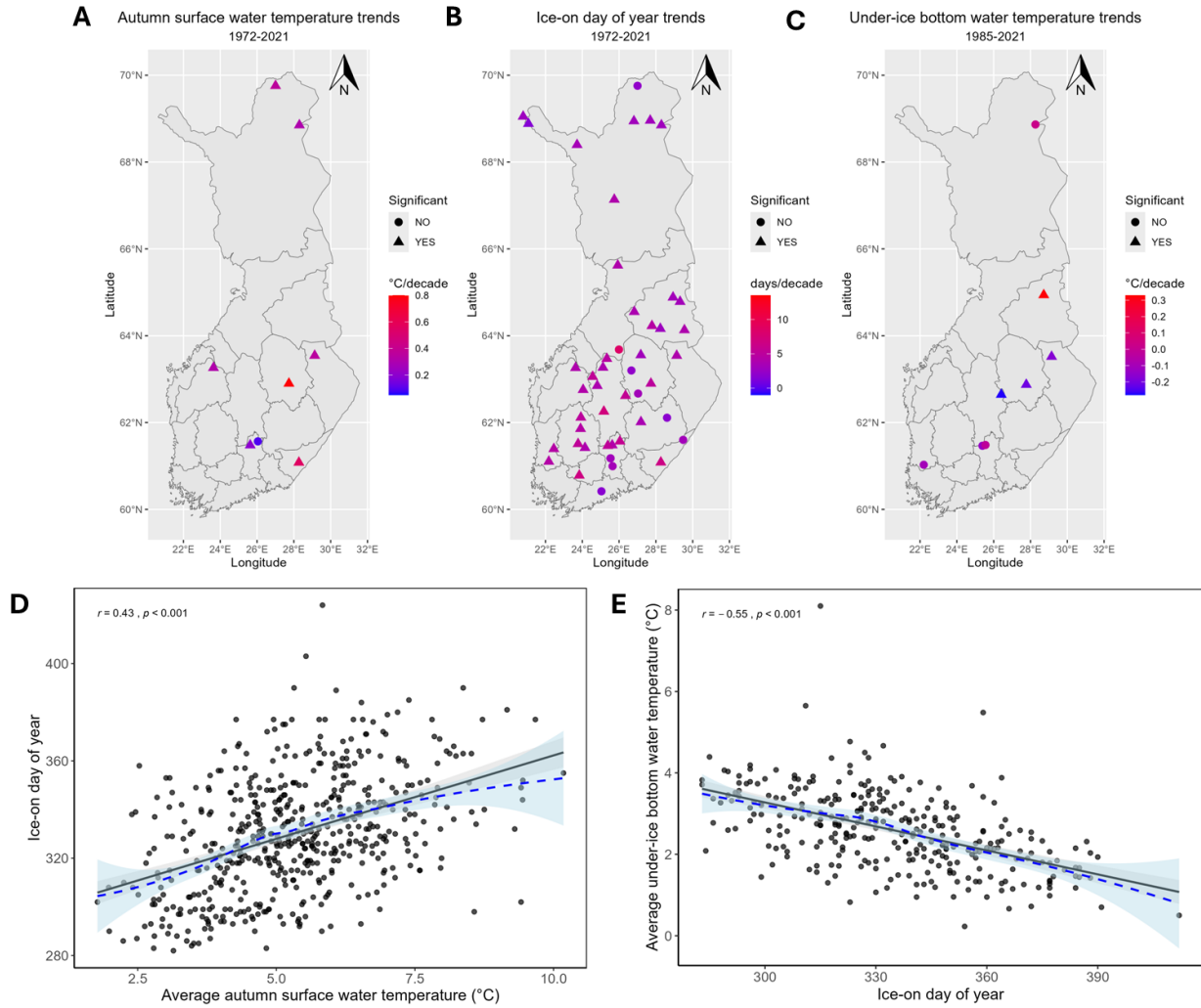


Figure 2. Long-term trends and relationships among autumn surface water temperature, ice-on date (calculated as day of year), and under-ice bottom water temperature in Finnish lakes.

Monotonic trends were assessed using the Mann-Kendall test with Theil-Sen's slope estimates ($p < 0.05$) for (A) autumn surface water temperature (October 1st to ice-on date) over 50 years, (B) ice-on date over 50 years, and (C) under-ice bottom water temperature over 37 years. Spearman's rank correlations were used to examine relationships between (D) autumn surface water temperature and ice-on date, and (E) ice-on date and under-ice bottom water temperature. Panels D and E include a linear regression fit (black line) and locally weighted smoothing (LOWESS;

blue dashed line) with shading indicating associated 95% confidence intervals. Note the different magnitudes within the legend bars in panels A-C.

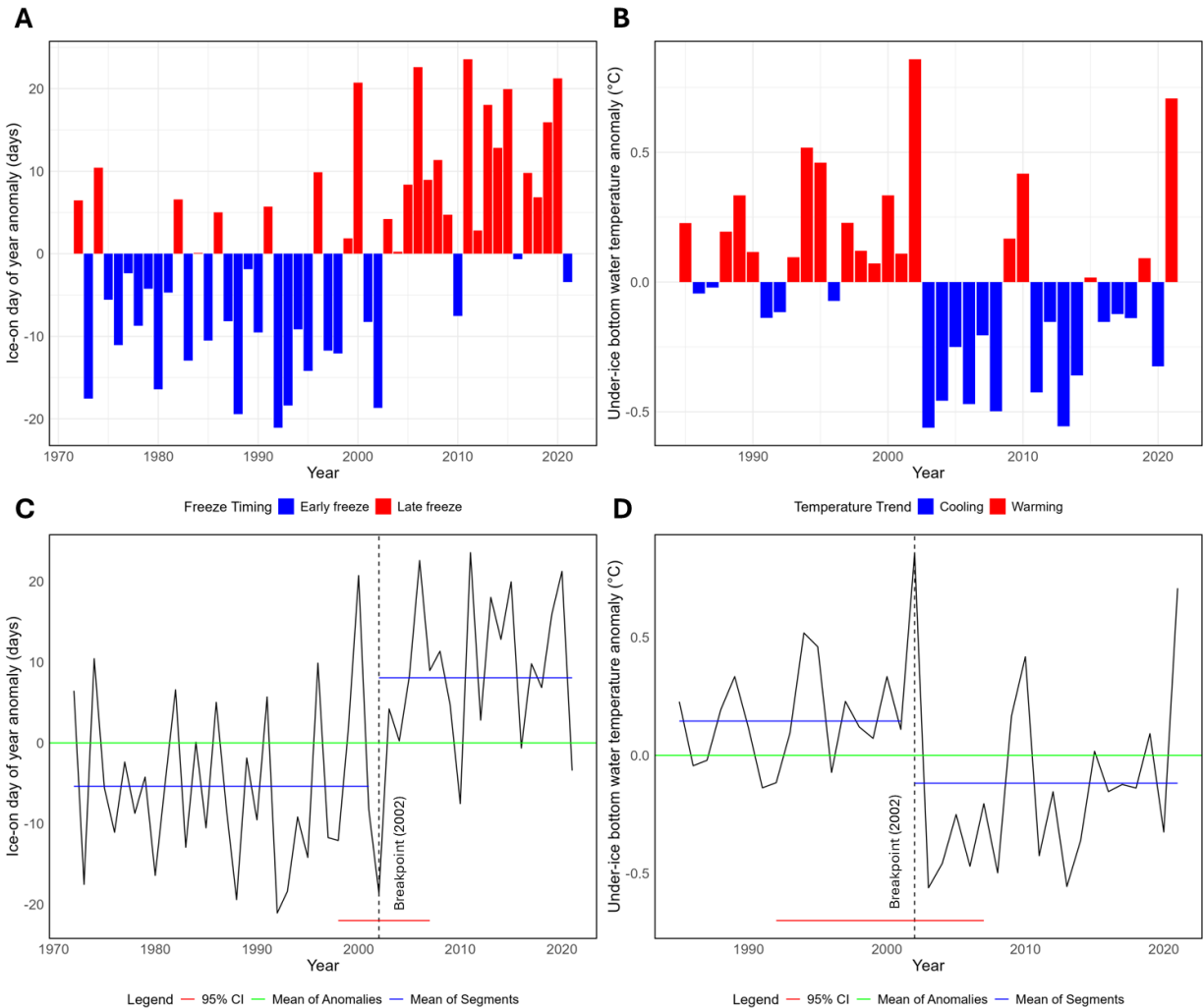


Figure 3. Long-term anomalies and breakpoints in ice-on date (calculated as day of year) and under-ice bottom water temperatures in Finnish lakes. Anomalies of (A) ice-on date from 1972 to 2021, calculated relative to the 50-year mean of November 26th (i.e., ordinal day 330) and (B) under-ice bottom water temperature from 1985 to 2021, calculated relative to the 37-year mean of 2.58 °C. Time series of (C) ice-on anomalies and (D) under-ice water temperature anomalies, with segmented means before and after identified breakpoints, and associated 95% confidence intervals.

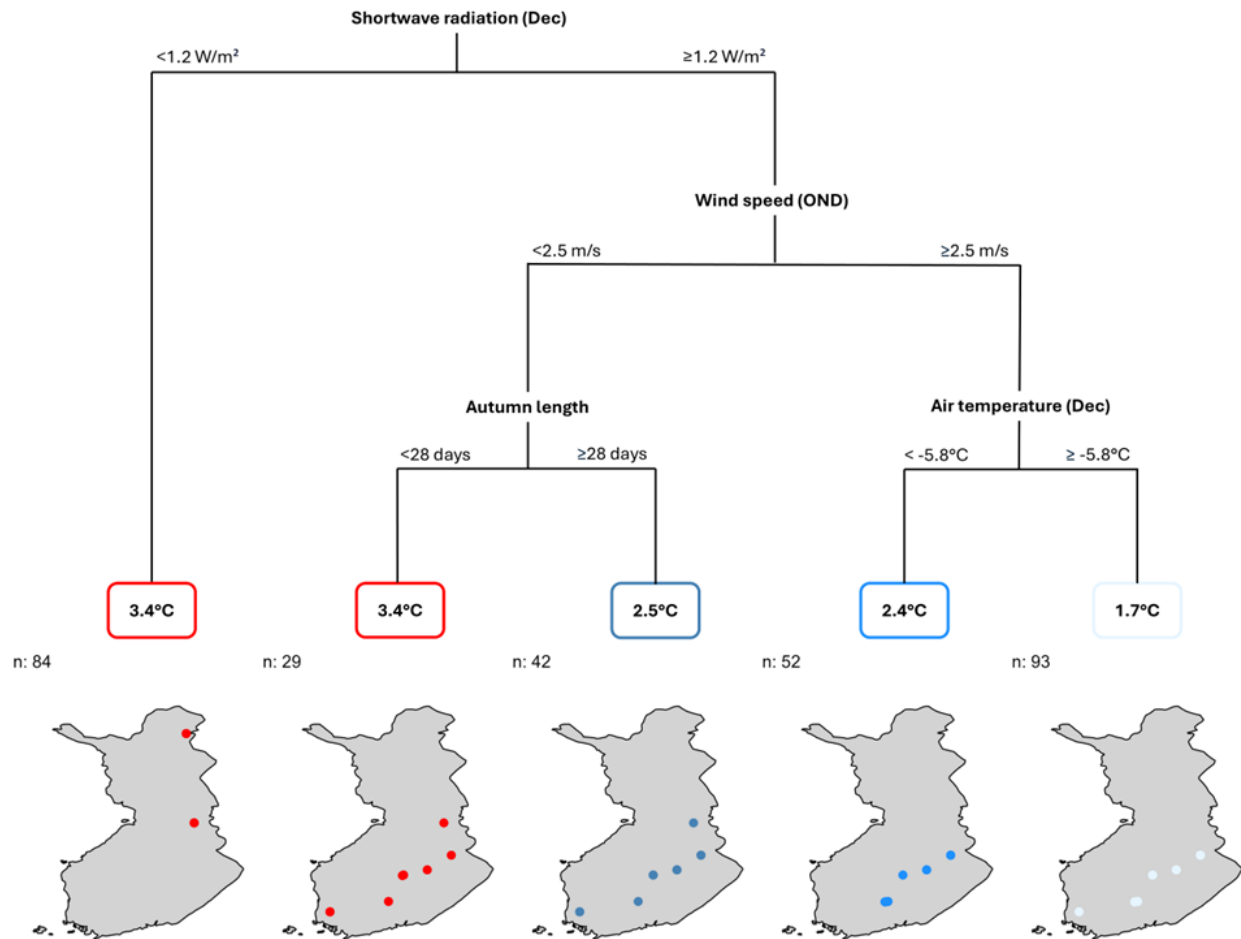


Figure 4. Regression tree predicting average under-ice bottom water temperature based on lake morphology, autumn dynamics, and autumn and early winter meteorological variables in 9 sites across Finland. n represents the number of yearly observations in each node, and maps below each terminal node illustrate where individual observations occurred.

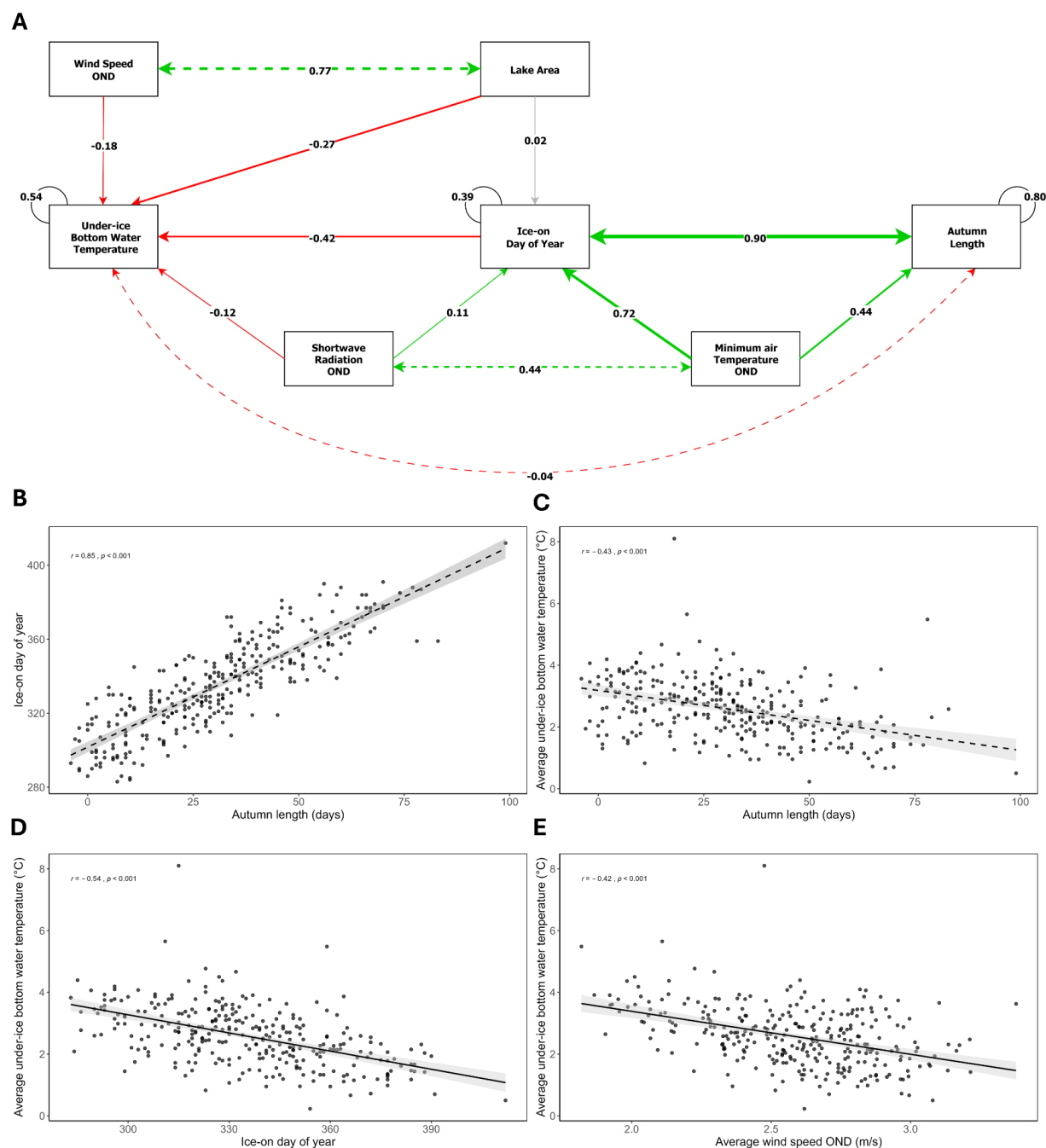


Figure 5. Structural equation model illustrating: (A) the relationships between autumn meteorological variables, lake morphology, and autumn seasonal dynamics in predicting average under-ice bottom water temperature, ice-on date (calculated as day of year), and autumn length in 9 sites across Finland. Solid arrows represent hypothesized causal pathways, with standardized

path coefficients indicating the strength and direction of relationships. Double-headed arrows indicate covariance between variables, while dashed, double-headed arrows represent covariance relationships added by the model. Non-significant paths are shown in grey. From the structural equation modeling data, Spearman's rank correlations are displayed for four selected relationships, including (B) autumn length and ice-on date, (C) autumn length and under-ice bottom water temperatures, (D) ice-on date and under-ice bottom water temperatures, and (E) wind speed and under-ice bottom water temperature to illustrate both total and indirect effects. Black lines represent linear fits, while the grey shading indicates the 95% confidence interval. Dashed regression lines are shown for relationships modeled solely as covariances in the structural equation model. Model fit: RMSEA: 0.044, SRMR: 0.029, CFI: 0.997, TLI: 0.992, χ^2 : 0.162.

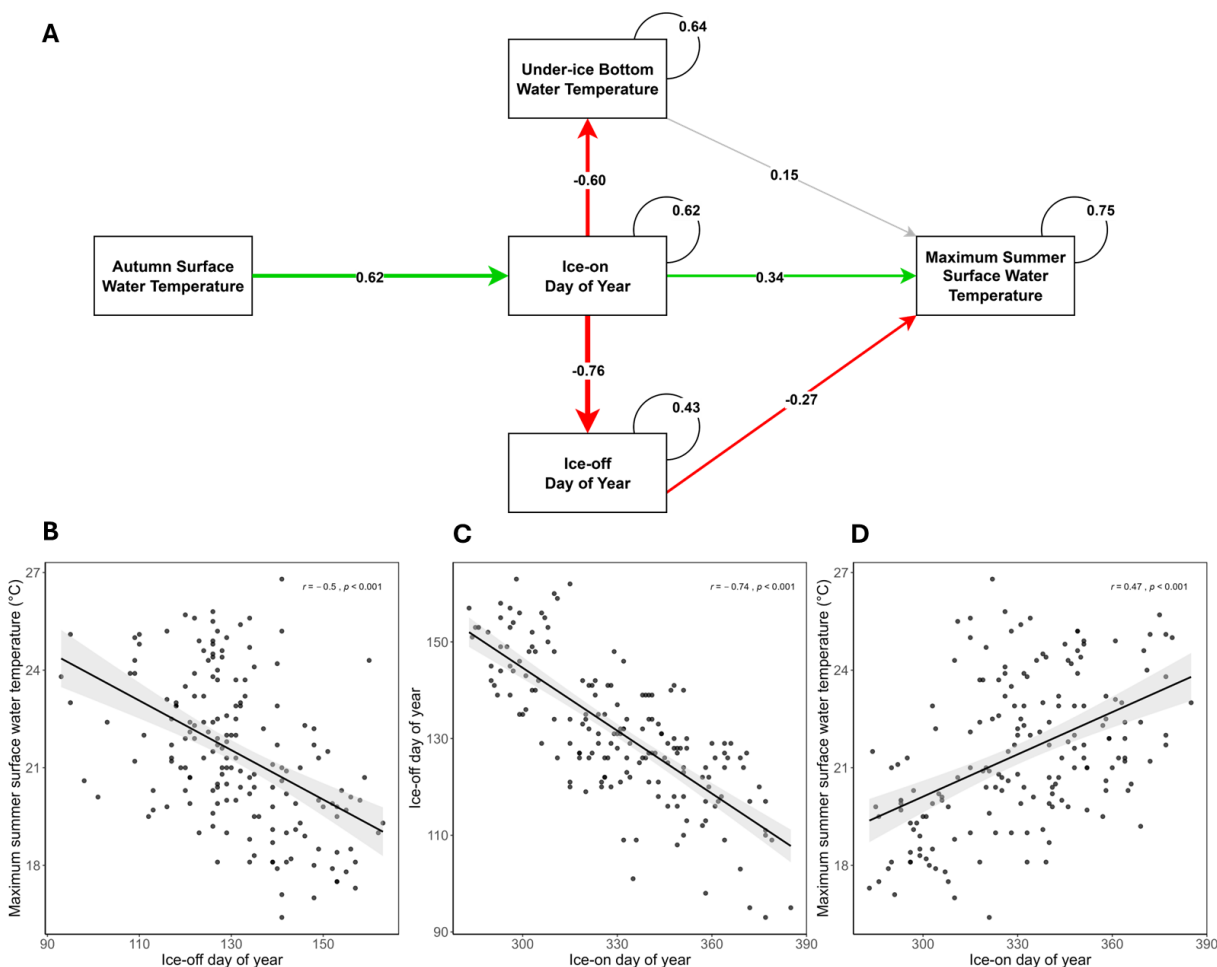


Figure 6. Structural equation model illustrating (A) the cross-seasonal relationships between autumn and winter water temperatures, ice phenology, and summer maximum surface water temperature in 5 lakes across Finland. Ice-on and ice-off dates were numerically expressed as day of year for analyses. Solid arrows represent hypothesized causal pathways, with standardized path coefficients that indicate the strength and direction of relationships. Non-significant relationships are shown in grey. From the structural equation modeling data, Spearman's rank correlations are displayed for three selected relationships, including (B) ice-off date and maximum summer surface water temperature, (C) ice-on date and ice-off date, and (D) ice-on date and maximum summer surface water temperature. Black lines represent linear fits and grey

shading indicates 95% confidence intervals. Model fit: SRMR: 0.043, CFI: 0.99, TLI: 0.96, χ^2 : 0.053.

Supplementary Information

Missing ice data for Lake Pesiöjärvi

Among the 9 sites with under-ice water temperature data, one site (*Lake Pesiöjärvi*) had missing ice data, making it challenging to determine the average under-ice water temperature, as ice-on and ice-off dates are needed for accurate calculations. To address the missing ice-on and ice-off dates for Lake Pesiöjärvi, we developed a methodology combining satellite imagery, temperature records, and freezing degree day (FDD) calculations (Supplementary Material).

Estimating ice-on dates was particularly challenging for *Lake Pesiöjärvi* due to the polar night, which rendered satellite images too dark to detect ice formation. Consequently, we used freezing degree days (FDD) as a proxy for ice formation, calculated by summing the absolute daily mean air temperature below 0°C, beginning at the first occurrence of mean temperatures below 0°C (Blagrove and Sharma 2023). Based on Blagrove and Sharma (2023), a threshold of 78 FDD was used to indicate likely ice-on dates. Biweekly surface water temperature measurements provided additional context, with temperature drops (e.g., from 2.0°C to 0.2°C) indicating the likely window of freezing. In cases when the calculated 78 FDD date fell within the observed water temperature window, the 78 FDD date was used as the ice-on date. However, in 4 of the 37 years, the 78 FDD date occurred before the observed cooling range, suggesting premature ice formation estimates (ex. surface water temperatures were still >2°C). In these cases, we used the median date observed within the water temperature window, as it was more consistent with lake thermal behavior approaching ice-on.

Estimating ice-off dates was less challenging as polar night did not affect the availability of satellite imagery. We analyzed satellite imagery using Sentinel Hub, utilizing Landsat data from 1987 to 2000 and MODIS Terra data from 2000 to 2021. This allowed us to identify a range, with the last image of ice cover and the first image without ice cover for the lake, in each

season. Biweekly surface water temperature measurements provided additional context, with rising temperatures (e.g., from 0.2°C to 2.0°C) indicating the likely window of thaw. When there was overlap between the satellite imagery range and the water temperature range, we took the median date within the overlap as the ice-off date. In 4 years, however, no such overlap occurred, where satellite imagery showed a later thaw range than indicated by water temperature profiles. Manual review of these cases revealed that surface water temperatures had already exceeded 3°C and the water column exhibited weak or no inverse stratification, conditions incompatible with ice cover. Given our goal was to estimate ice cover period, we used the median date within the water temperature range because cloud-obstructed images rendered the satellite images less reliable. By integrating multiple data sources, we developed robust estimates of ice-on and ice-off dates for Pesiöjärvi, enabling the inclusion of this site in analyses of under-ice water temperatures and associated trends.

Table S1. Sites (lake name + location) and trends in autumn surface water temperature (averaged from October 1st to ice-on) from 1972-2021, with associated p-values.

Site Name	Sen's Slope (°C/decade)	p-value
Inari Nellim	0.31	0.0046
Jääsjärvi Hartola	0.09	0.51
Kallavesi Kuopio	0.79	0.000000012
Kevojärvi Kevoniemi	0.36	0.000058
Lappajärvi Halkosaari	0.31	0.0086
Päijänne Sysmä	0.20	0.042
Pielinen Nurmes	0.35	0.0029
Saimaa Lauritsala	0.55	0.0000021

Table S2. Changes in monotonic trends were calculated using Mann-Kendall and Sen's slope.

Sites (lake name + location) and trends in ice-on date from 1997-2021 and 1972-2021, with associated p-value. Changes in monotonic trends were calculated using Mann-Kendall and Sen's slope.

Site name	<i>1997-2021</i>		<i>1972-2021</i>	
	Sen's Slope (days/decade)	p-value	Sen's Slope (days/decade)	p-value
Ähtärinjärvi Niemiaho	0.80	0.080	4.19	0.018
Haukivesi Oravi	0.35	0.035	1.86	0.22
Iisvesi Suonenjoki	0.52	0.052	3.18	0.068
Inari Nellim	5.28	0.53	2.96	0.0099
Inari Selkävedet	5.43	0.54	3.06	0.044
Jääsjärvi Hartola	0.76	0.076	5.71	0.0010
Kallavesi Kuopio	1.17	0.12	5.00	0.0017
Kevojärvi Kevoniemi	8.15	0.82	2.17	0.068
Kianta Ämmänsaari	3.44	0.34	3.16	0.0041
Kilpisjärvi Kilpisjärvi	5.43	0.54	2.86	0.0015
Kivijärvi Saarenkylä	1.35	0.13	3.85	0.0030
Konnevesi Etelä	1.28	0.13	5.56	0.0035
Kuivajärvi Saari	0.44	0.044	6.67	0.0024
Kyyjärvi Kyyjärvi	0.84	0.084	5.33	0.00073
Kyyvesi Haukivuori	0.02	0.0019	3.64	0.0066
Lammasjärvi Kuhmo	2.39	0.24	3.93	0.0012
Längelmävesi Kaivanto	0.88	0.088	3.89	0.045

Lappajärvi Lappajärvi	4.40	0.44	4.00	0.017
Mutusjärvi Riutula	7.43	0.74	3.00	0.0017
Muurasjärvi Pihitpudas	1.83	0.18	4.72	0.0030
Näsijärvi Tampere	1.83	0.18	5.24	0.014
Nuasjärvi Vuokatti	0.48	0.048	2.86	0.019
Oijärvi Matilanjärvi	6.91	0.69	4.07	0.0013
Oulujärvi Vaala	0.55	0.055	3.75	0.0032
Ounasjärvi Hetta	0.39	0.039	3.33	0.00046
Pääjärvi Karstula	0.97	0.097	3.85	0.022
Päijänne Sysmä	3.15	0.31	4.17	0.045
Päijänne Tehi	7.97	0.80	5.24	0.0080
Päijänne Vääksy	5.75	0.57	3.71	0.051
Palovesi Murole	3.38	0.34	4.44	0.035
Peerajärvi Enontekiö	3.85	0.39	1.54	0.027
Petäjävesi Petäjävesi	0.10	0.010	7.00	0.00044
Pielavesi Säviä	2.07	0.21	2.14	0.083
Pielinen Nurmes	0.26	0.026	4.00	0.0052
Porovesi Iisalmi	0.44	0.044	3.08	0.023
Pyhäjärvi Kauttua	0.64	0.064	4.35	0.011
Pyhäjärvi Pyhäsalmi	1.12	0.11	8.40	0.000012
Rehja Kajaani	0.61	0.061	4.50	0.0028
Sääksjärvi Sääkskoski	0.20	0.020	4.44	0.0070
Saimaa Lauritsala	3.74	0.37	6.54	0.0013
Simpelejärvi Parikkala	0.49	0.049	3.13	0.086
Tuusulanjärvi Tuusula	2.52	0.25	1.79	0.31

Unari Sodankylä	3.25	0.33	4.00	0.00031
Vesijärvi Lahti	1.98	0.20	3.24	0.050
Vesijärvi Vääksy	2.62	0.26	3.08	0.094
Visuvesi Kanava	1.99	0.20	5.00	0.0084
Vuokkijärvi Sankki	1.77	0.18	3.18	0.0052

Table S3. Sites (lake name + location) and trends in under-ice bottom water temperature from 1985 to 2021, with associated p-values. Changes in monotonic trends were calculated using Mann-Kendall and Sen's slope.

Site name	Sen's Slope (°C/decade)	p-value
Kallavesi Säyneensalo	-0.21	0.0079
Pielinen Nurmes	-0.17	0.047
Päijänne Linnasaari	-0.14	0.24
Päijänne Päijätsalo	-0.02	0.78
Konnevesi Näreselkä	-0.27	0.0015
Pyhäjärvi Säkylä	-0.10	0.17
Pesiöjärvi Suomussalmi	0.32	0.00094
Inari Paksuvuono	0.02	0.82

Table S4. Sites (lake name + location) and associated coordinates for surface water temperature, ice phenology, and under-ice water temperature monitoring locations.

	Site Name	Latitude	Longitude
<i>Ice phenology sites</i>	Simpelejärvi Parikkala	61.60082	29.48246
	Pielinen Nurmes	63.54181	29.13139
	Porovesi Iisalmi	63.55497	27.18093
	Kallavesi Kuopio	62.89926	27.73173
	Haukivesi Oravi	62.11074	28.6064
	Saimaa Lauritsala	61.08318	28.27196
	Muurasjärvi Pihtipudas	63.47117	25.33519
	Kivijärvi Saarenkylä	63.26701	25.12644
	Kyyjärvi Kyyjärvi	63.05553	24.56513
	Pääjärvi Karstula	62.84741	24.81424
	Pielavesi Säviä	63.1993	26.66959
	Iisvesi Suonenjoki	62.66811	27.03301
	Konnevesi Etelä	62.61658	26.34922
	Petäjavesi Petäjavesi	62.25546	25.17325
	Jääsjärvi Hartola	61.56738	26.04671
	Päijänne Sysmä	61.47868	25.62781
	Vesijärvi Lahti	60.99462	25.64813
	Vesijärvi Vääksy	61.17603	25.53621
	Päijänne Vääksy	61.17652	25.5371
	Kyyvesi Haukivuori	62.01271	27.18946
	Päijänne Tehi	61.46523	25.38819
	Tuusulanjärvi Tuusula	60.41678	25.04273

	Pyhäjärvi Kauttua	61.10153	22.18018
	Längelmävesi Kaivanto	61.41801	24.14743
	Ähtärinjärvi Niemiaho	62.75534	24.04539
	Visuvesi Kanava	62.1175	23.92487
	Palovesi Murole	61.8557	23.90679
	Näsijärvi Tampere	61.50856	23.77253
	Kuivajärvi Saari	60.78213	23.83833
	Sääksjärvi Sääkskoski	61.39379	22.45437
	Lappajärvi Lappajärvi	63.25948	23.63529
	Pyhäjärvi Pyhäsalmi	63.68173	25.99451
	Kianta Ämmänsaari	64.88325	28.93181
	Vuokkijärvi Sankki	64.78382	29.31395
	Lammasjärvi Kuhmo	64.13125	29.55098
	Nuasjärvi Vuokatti	64.16164	28.2441
	Rehja Kajaani	64.22694	27.78728
	Oulujärvi Vaala	64.55092	26.82401
	Oijärvi Matilanjärvi	65.62058	25.93016
	Ounasjärvi Hetta	68.3975	23.71696
	Unari Sodankylä	67.13658	25.74154
	Kilpisjärvi Kilpisjärvi	69.04976	20.78807
	Peerajärvi Enontekiö	68.88332	21.07637
	Kevojärvi Kevoniemi	69.75659	27.00316
	Mutusjärvi Riutula	68.94339	26.80664
	Inari Nellim	68.84999	28.30071
	Inari Selkävedet	68.95772	27.6942

<i>Under-ice water temperature sites</i>	Kallavesi Säyneensalo	62.87267	27.77022
	Pielinen Nurmes	63.51758	29.14766
	Päijänne Linnasaari	61.46523	25.38819
	Päijänne Päijätsalo	61.48323	25.55231
	Konnevesi Näreselkä	62.64399	26.41098
	Konnevesi Pynnölänniemi	62.62269	26.35004
	Pyhäjärvi Säkylä	61.02728	22.20004
	Pesiöjärvi Suomussalmi	64.93749	28.72093
	Inari Paksuvuono	68.86549	28.26819
<i>Surface water temperature sites</i>	Haukivesi Oravi	62.1132	28.60754
	Nuasjärvi Vuokatti	64.16369	28.23893
	Pielinen Nurmes	63.54181	29.13139
	Kallavesi Kuopio	62.89938	27.73161
	Saimaa Lauritsala	61.07948	28.27342
	Jääsjärvi Hartola	61.56638	26.04661
	Päijänne Sysmä	61.47864	25.62766
	Pielavesi Säviä	63.19922	26.66987
	Lappajärvi Halkosaari	63.2608	23.63202
	Oijärvi Ii	65.62218	25.93059
	Inari Nellim	68.85	28.30056

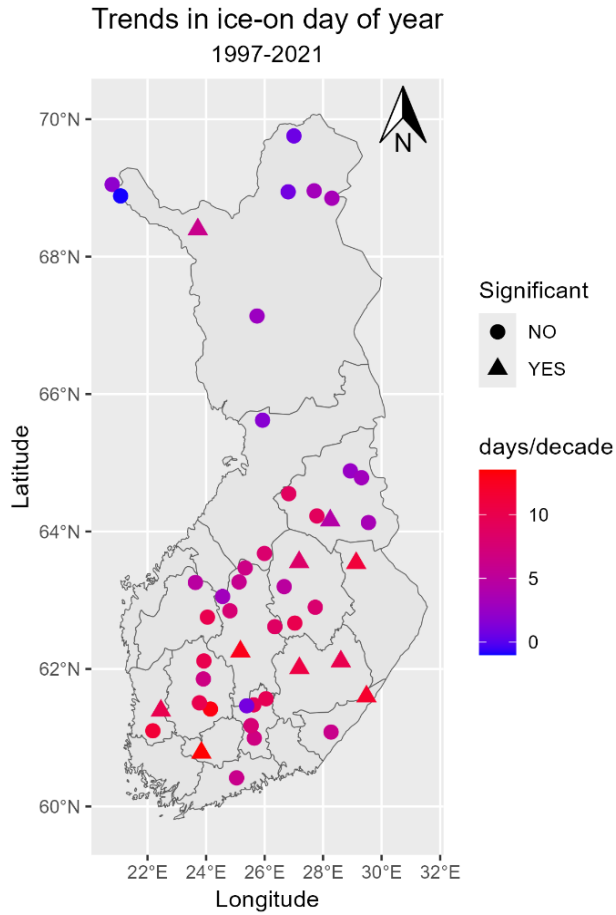


Figure S1. Trends in ice-on date (calculated as day of year) in lakes across Finland calculated over a 25-year time interval, from 1997 to 2021. Monotonic trends were identified using the Mann-Kendall test, with trend magnitudes calculated using Sen's slope method.

Non-significant relationships are shown in grey. Model fit: SRMR: 0.38, CFI: 0.75, TLI: 0.53, χ^2 : 0.0.

Non-significant relationships are shown in grey. Model fit: SRMR: 0.38, CFI: 0.75, TLI: 0.53, χ^2 :

General conclusion

This thesis evaluated the ecological significance of autumn in lake ecosystems, with a focus on how shifting autumn conditions influence winter and cross-seasonal dynamics. In the first chapter, *Autumn as an Overlooked Opportunity for Limnology*, we synthesized current literature and found that autumn is the least studied season within limnology. Autumn has represented a maximum of 10% of limnological studies annually since 2000, with this proportion remaining consistent over the last two decades, despite its critical role in thermal regimes, nutrient cycling, and biological productivity. We provide a clear set of definitions for autumn used in limnology and address inconsistencies within literature that may hinder autumnal research. This chapter established a framework for understanding how climate driven shifts in autumn may affect ecosystems across seasons, emphasizing the need to better incorporate autumn dynamics into limnological research.

Building on this foundation, the second chapter examines empirical data on autumn and winter lake processes in 47 lakes across Finland. Our analysis revealed significant warming of autumn summer water temperatures, delayed ice formation, and cooling of bottom under-ice temperatures. These observed shifts are causally linked, such that warmer autumns extend the period of pre-freeze heat loss, delaying ice-on, and resulting in colder under-ice conditions. These findings provide amongst the first empirical assessments of how autumn conditions indirectly govern winter thermal regimes, a previously overlooked seasonal linkage. This work highlights autumn as a pivotal transitional period, where processes such as wind-driven mixing and the duration of pre-freeze heat loss collectively shape under-ice conditions, with cascading effects that may extend into summer. This chapter advances our understanding of cross seasonal

linkages in dimictic lakes, reinforcing the need to include autumn in limnological research to better understand year-round lake dynamics in a changing climate.

Future research should build on this work by integrating autumn dynamics into cross-seasonal lake models. Processes such as the duration of heat loss and the timing of mixing events are essential for predicting ice phenology patterns, under-ice thermal structure, and associated ecosystem responses. However, to effectively integrate autumn into our understanding of lake responses to climate change, improvements in the duration and frequency of sampling are needed. Expanding monitoring efforts to include high frequency measurements through late autumn and into winter is imperative. Broader spatial coverage, including lakes of varying size, depth, and location, is also needed to assess how consistently different lake types respond to seasonal patterns. Ultimately, strengthening observational coverage and model integration across seasons will be essential to anticipate how lakes will respond to ongoing warming.

Together these chapters show that autumn plays a critical role in shaping lake conditions in a warming world. As temperatures continue to rise, seasonal lake processes will shift, with changes in the breakdown of stratification and timing of autumn mix driving cascading effects on ecosystem function. While much of limnological research has traditionally focused on spring and summer, this work highlights the critical influence of the autumn season. As lakes continue to change in response to global warming, understanding year-round ecosystem dynamics will be vital to anticipate future impacts on aquatic ecosystems.