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Lake food webs under changing winter conditions

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Abstract
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At northern latitudes, lakes are ice-covered for several months every year, and winter has long been viewed as an ecologically dormant period. However, biological processes continue beneath the ice, and the conditions during ice cover can shape lake food webs into spring. This thesis examines how ice cover and winter conditions structure lake food webs, with a particular focus on the drivers of phyto- and zooplankton growth under ice. Through a combination of literature synthesis, long-term monitoring, and experimental and field studies, the work investigates how ice cover, winter precipitation and runoff, and habitat-specific processes. influence productivity and trophic interactions below ice. One main finding was that snow cover and ice quality (black versus white ice) are critical predictors of under-ice phytoplankton growth (paper I-II). Reduced light transmission through snow limited phytoplankton biomass and shifted community composition toward mixotrophic taxa. Further, the duration of ice cover influenced spring dynamics, where shorter ice-covered periods reduced the magnitude of the spring phytoplankton bloom (paper I-II). These findings highlight that both the duration and composition of the ice cover set the conditions for winter and spring productivity in lakes. Furthermore, the timing and magnitude of runoff were found to shape under-ice food webs. Experimental manipulations showed that early nutrient inputs under low-light conditions promoted mixotrophs, while later inputs supported stronger spring phytoplankton blooms (paper III). Field observations indicated that terrestrial organic matter inputs reduced the nutritional quality of basal resources during winter. In lakes with high terrestrial organic matter availability, copepods incorporated more terrestrial and bacterial resources but maintained nutritional quality (paper IV). Finally, spatial analyses revealed pronounced habitat heterogeneity in winter resources, with littoral habitats enriched in terrestrial and bacterial organic matter, and pelagic habitats dominated by algal-derived organic matter. These differences were reflected in copepods (paper IV), demonstrating that resource heterogeneity under ice is transferred to higher trophic levels. Together, the findings of this thesis highlight winter as a dynamic period in lake ecosystems. Climate-driven shifts in ice phenology, ice quality, and winter runoff may increase heterotrophy and reduce resource quality, weakening energy transfer to higher trophic levels and altering lake carbon cycling.

Keywords: Ice cover, bacteria, phytoplankton, zooplankton, light, nutrients, runoff

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"It's still magic even if you know how it's done." – Terry Pratchett

List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

I. Culpepper, J., Jakobsson, E., Weyhenmeyer, G.A., Hampton, S.E., Obertegger, U., Shchapov, K., Woolway, R.I, Sharma, S. (2024) Lake ice quality in a warming world. *Nature Reviews Earth & Environment* 5(10):671–685

II. Jakobsson, E., Langenheder, S., Eklöv, P., Weyhenmeyer, G.A. (2025) Effects of changing snow and ice cover conditions on phytoplankton chlorophyll-*a* and community composition in a mesotrophic lake. *Freshwater Biology* 70(3):e70012

III. Jakobsson, E., Vikström, K., Langenheder, S., Pierson, D., Weyhenmeyer, G.A. (2025) Timing of nutrient inputs during ice cover regulates lake spring plankton dynamics. Under review in *Limnology and Oceanography.*

IV. Jakobsson, E., Rijnsburger, E., Chaguaceda, F., Vikström, K., Eklöv, P., Weyhenmeyer, G.A. (2025) Spatial heterogeneity in copepod resource use under ice. *Manuscript*.

Additional Papers

The following papers were published or submitted during my doctoral studies but are not part of this thesis.

- Weyhenmeyer, G.A., Obertegger, U., Rudebeck, H., Jakobsson, E., Jansen, J., Zdorovennova, G., Bansal, S., Block, B.D., Carey, C.C., Doubek, J.P., Dugan, H., Erina, O., Fedorova, I., Fischer, J.M., Grinberga, L., Grossart, H.-P., Kangur, K., Knoll, L.B., Laas, A., Lepori, F., Meier, J., Palshin, N., Peternell, M., Pulkkanen, M., Rusak, J.A., Sharma, S., Wain, D., Zdorovennov, R. (2022) Towards critical white ice conditions in lakes under global warming. *Nature Communications* 13(1):4974
- Fehlinger, L., Misteli, B., Morant, D., Juvigny-Khenafou, N., Cunillera-Montcusí, D., Chaguaceda, F., Stamenković, O., Fahy, J., Kolář, V., Halabowski, D., Nash, L.N., Jakobsson, E., Nava, V., Tirozzi, P., Urrutia-Cordero, P., Mocq, J., Santamans, A.C., Zamora-Marín, J.M., Marle, P., Chonova, T., Bonacina, L., Mathieu-Resuge, M., Suarez, E., Osakpolor, S.E., Timoner, P., Evtimova, V., Nita, D., Carreira, B.M., Tapolczai, K., Martelo, J., Gerber, R., Dinu, V., Henriques, J., Selmeczy, G.B., Rimcheska, B. (2023) The ecological role of permanent ponds in Europe: a review of dietary linkages to terrestrial ecosystems via emerging insects. *Inland Waters* 13(1):30–46
- Reinl, K.L., Harris, T.D., North, R.L., Almela, P., Berger, S.A., Bizic, M., Burnet, S.H., Grossart, H.-P., Ibelings, B.W., Jakobsson, E., Knoll, L.B., Lafrançois, B.M., McElarney, Y., Morales-Williams, A.M., Obertegger, U., Ogashawara, I., Paule-Mercado, M.C., Peierls, B.L., Rusak, J.A., Sarkar, S., Sharma, S., Trout-Haney, J.V., Urrutia-Cordero, P., Venkiteswaran, J.J., Wain, D.J., Warner, K., Weyhenmeyer, G.A., Yokota, K. (2023) Blooms also like it cold. *Limnology and Oceanography Letters* 8:546–564
- Vikström, K., Weyhenmeyer, G.A., Jakobsson, E., Peternell, M. (2025) Rapid lake ice structure changes across Swedish lakes puts public ice safety at risk. *Ambio* 54(1):122–134
- Fehlinger, L., Chaguaceda, F., Tirozzi, P., Tomás-Martín, M., Jakobsson, E., Chonova, T., Misteli, B., Scotti, A., Henriques, J.F., Rubio-Ríos, J., Morant, D., Marle, P., Kolar, V., Stamenković, O., Mondav, R., Münzner, K., Osakpolor, S.E., Bonacina, L., Nava, V., Drohan, E., Fenoy, E., Llorente, A., Mathieu-Resuge, M., Halabowski, D., Juvigny-Khenafou,

N.P.D., Martelo, J., Nash, L., Fahy, J.C., Cunillera-Montcusí, D., Balibrea, A., Rimcheska, B. (2025) Nutrients on the move: Investigating large scale fatty acid exports from European ponds via emerging insects. *Limnology and Oceanography* 70(10):2844–2857

- Donini, G., Agostinelli, C., Weyhenmeyer, G.A., Kirillin, G., Leppäranta, M., Zdorovennova, G., Aslamov, I.A., Culpepper, J.A., Dugan, H.A., Fedorova, I.V., Jakobsson, E., North, R.L., Novikova, I., Palshin, N., Pearce, N.J., Robinson, J., Shchapov, K., Vikström, K., Xenopoulos, M., Yang, X., Zdorovennov, R., Piccolroaz, S. Bayesian estimates of ice optical properties for lake ice modelling. (2025) *Geophysical Research Letters* (Under review)

Contents

Abbreviations

ARA	Arachidonic acid
CCA	Canonical correlation analysis
Chl-*a*	Chlorophyll *a*
DF	Delayed fluorescence
DHA	Docosahexaenoic acid
DO	Dissolved oxygen
DOC	Dissolved organic carbon
DOM	Dissolved organic matter
EPA	Eicosapentaenoic acid
FA	Fatty acid
GAMM	Generalized additive mixed model
LME	Linear mixed-effect (model)
PAR	Photosynthetically active radiation
P–I	Photosynthesis–Irradiance
pRDA	Partial redundancy analysis
PUFA	Polyunsaturated fatty acids
SAFA	Saturated fatty acids
SUVA	Specific UV absorbance

Introduction

Lake food webs

Food webs describe how energy and nutrients move among organisms through consumption and production. In freshwater systems such as lakes, these interactions involve diverse groups ranging from microorganisms to fish, collectively regulating ecosystem productivity and nutrient cycling. Food webs in lakes can differ in complexity depending on, for example, the trophic status of the lake or the habitat within the lake (Polis and Strong, 1996; Embke and Zanden, 2022). Lake food webs support several trophic levels and are easier understood when conceptualized (Fig. 1). Simplified, primary producers such as phytoplankton or macrophytes get their energy from photosynthesis and constitute the "green pathway" in lakes, commonly referred to as autochthonous production (Wetzel, 2001; Cole et al., 2002). Primary producers are grazed upon by, among others, a range of intermediate invertebrate predators, such as zooplankton or benthic invertebrates (Fig. 1). Lastly, organisms which predate upon these lower trophic levels while not being predated upon by any higher trophic levels make up the top predators within the food web, usually different fish species. Overall, these interactions among trophic levels support different energetic pathways within the food web (Lindeman, 1942). Bacteria and heterotrophic protists also play an essential role in the circulation of energy and nutrients within lake food webs through the microbial loop (Azam et al., 1983). Bacteria, for example, break down dissolved organic matter (DOM) released by organisms, such as through excretion or cell lysis (Thornton 2014; Johnston et al. 2022; Fig. 1). The bacterial degradation of DOM is particularly important as it regenerates essential nutrients that are taken up by primary producers (Li et al., 2014). In addition to autochthonous production, inputs of terrestrial organic matter are often referred to as allochthonous resources and can play a central role in supporting lake food webs (Wetzel 2001; Cole et al. 2002; Fig. 1). Allochthonous resources can be especially important in lakes where these are relatively more abundant than autochthonous production (Tanentzap et al., 2017), and particularly in lakes with forested catchments (Keva et al., 2025). Specifically, nutrients and carbon from terrestrial sources can sustain bacterial growth, which in turn supports higher trophic levels through the microbial loop (Fig. 1). The relative importance of allochthonous and autochthonous resources in supporting lake food webs also varies spatially within lakes. For example, food webs in open-water (pelagic) habitats tend to rely more on autochthonous production (Wetzel, 2001; Reynolds, 2006), whereas shoreline (littoral) habitats often receive large inputs of terrestrial organic matter, resulting in a greater dependence on allochthonous resources (Vadeboncoeur, Vander Zanden and Lodge, 2009; Solomon et al., 2011, 2015).

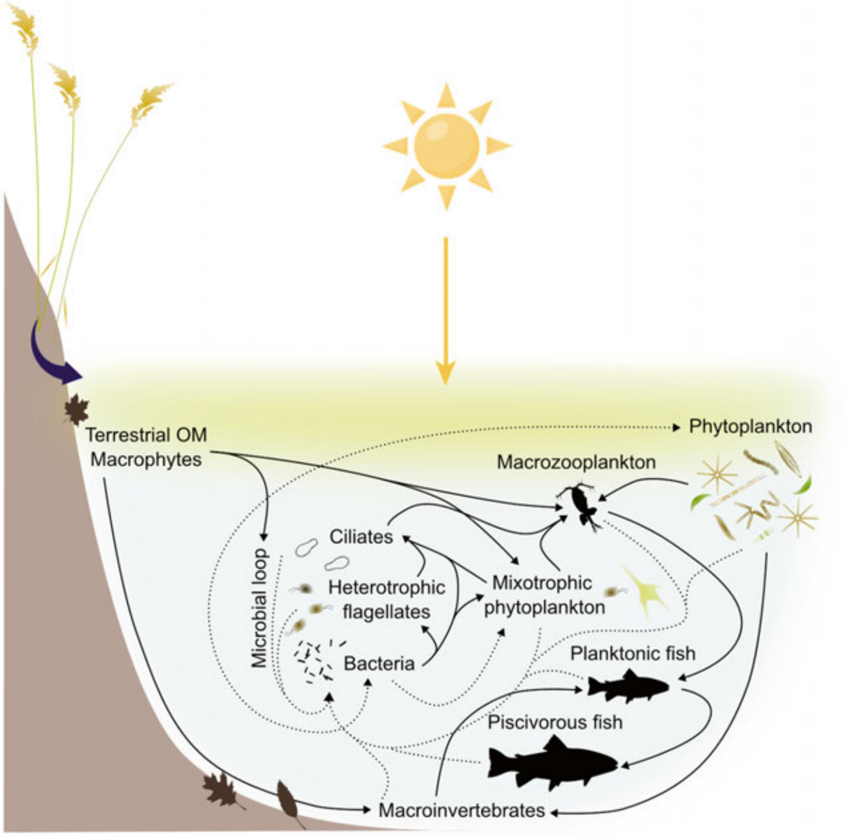

Figure 1. Conceptual overview of a simplified lake food web showing autochthonous (phytoplankton-derived) production and allochthonous (terrestrially-derived) organic matter inputs, together with the microbial loop, fueling growth of intermediate predators and higher trophic levels. Predation and assimilation are indicated with solid arrows, and excretion processes are shown with dotted arrows.

Interactions across trophic levels in lake food webs can be regulated by either bottom-up or top-down control, depending on a range of physical, chemical and biological conditions (Carpenter, Kitchell and Hodgson, 1985; McQueen, Post and Mills, 1986). Bottom-up regulation is driven by changes occurring at lower trophic levels, such as primary producers, which drive changes at higher trophic levels. Exemplified, an increase in phytoplankton biomass may lead to an increase in biomass of herbivorous zooplankton which can increase the biomass of the top predator. Top-down control occurs when higher trophic levels, such as top predators, increase in biomass and regulate lower levels through predation. For example, a decrease in planktivorous fish from predation pressure can increase the abundance of herbivorous zooplankton which may decrease phytoplankton biomass. While bottom-up and top-down control are easily separated conceptually, they usually interplay concurrently and shifts can be observed within longer or shorter time frames (Carpenter and Kitchell, 1996). Such interactions between trophic levels shift over the year, usually in response to changing environmental conditions, as described by the Plankton Ecology Group (PEG) model (Sommer et al., 1986). Many lakes display bottom-up regulation following ice-out in spring, as phytoplankton growth increases in response to enhanced light availability after the disappearance of a snow- and ice cover (Sommer et al., 1986; Chiswell, Calil and Boyd, 2015). Such increases in light together with thermal stratification which concentrates nutrients in the euphotic zone can favor large, fast-growing phytoplankton taxa, for example diatoms. The rapid increase in phytoplankton biomass provides abundant high-quality food, supporting the development of herbivorous zooplankton populations (Sommer et al., 1986). The combination of the quantity, timing and quality of phytoplankton production plays a key role in determining zooplankton growth and reproduction (Sterner and Hessen, 1994; Winder and Schindler, 2004). As grazing pressure intensifies and nutrients are depleted, smaller, motile phytoplankton such as dinoflagellates and cyanobacteria become dominant. Finally, when stratification breaks down in autumn, mixing replenishes surface nutrients, promoting non-motile taxa like diatoms again (Sommer et al., 1986). Originally, the PEG model largely neglected biological activity during winter when lakes are ice- and snow covered (Sommer et al., 1986), likely due to a lack of information following the logistical challenges of winter sampling (Block et al., 2019). However, more recent work, including revisions of the PEG model, has emphasized the importance of under-ice processes, such as overwintering of key taxa and microbial interactions (Sommer et al., 2012; Bertilsson et al., 2013; Hampton et al., 2017).

Food webs in ice-covered lakes

At high latitudes, a large portion of lakes remain ice covered for several months every year. Ice cover influences lake thermal structure through inverse stratification with colder surface than bottom temperatures, limits gas exchange with the atmosphere and reduce light availability in the water column (Kirillin et al., 2012). Historically, these ice-covered periods were considered ecologically dormant, as low temperatures and low light availability were believed to suppress biological activity until spring thaw (Salonen et al., 2009). However, research over the past two decades has fundamentally challenged this assumption, revealing that food-web interactions are sustained during ice cover. Beneath the ice, bacteria, phytoplankton, and zooplankton, among other organisms, continue to grow and interact (Hampton et al., 2017) but yet, drivers of these interactions have been largely unexplored during ice cover. Specifically, light and nutrient regimes are considered two of the main drivers of food-web dynamics and during winter, the composition and phenology of the ice cover in combination with runoff events can shape these regimes with potential effects on under-ice food webs.

The structure of the ice cover and the presence of snow can shape the growth and composition of under-ice phytoplankton by altering light availability and water movement, with subsequent changes in nutrient distribution (Salmi and Salonen, 2016; Hampton et al., 2017; Jansen et al., 2021; Smith et al., 2025). White ice, characterized by high air content and low transparency, along with snow cover, significantly reduce light penetration into the water column (Bolsenga and Vanderploeg, 1992), reducing convective mixing (Smith et al., 2025) and thus, resuspension of nutrients to the photic zone. Such stagnant, low-light conditions favor motile, mixotrophic phytoplankton (Socha et al., 2023; Jakobsson et al., 2025), which can supplement photosynthesis with the uptake of organic particles as energy sources (Mitra et al., 2016). In contrast, clear ice, often referred to as black ice, transmits nearly all incoming light (Bolsenga and Vanderploeg, 1992), promoting convective mixing (Smith et al., 2025). High light availability under clear ice supports non-motile, autotrophic taxa (Jewson et al., 2009), which rely primarily on photosynthesis for their growth (Reynolds, 2006). These same physical conditions affecting phytoplankton dynamics can drive interactions within under-ice food webs. For example, phytoplankton blooms below ice can drive peaks in under-ice bacterial growth (Bižić-Ionescu, Amann and Grossart, 2014). Such increases in bacteria can provide an important resource for zooplankton grazers, especially at times of low phytoplankton availability (Taipale et al., 2008; Berggren, Bergström and Karlsson, 2015; Wenzel et al., 2021). Similarly, zooplankton growth under ice can be tightly coupled to phytoplankton availability with enhanced light conditions driving increases in zooplankton biomass (Bramm et al., 2009).

Apart from the ice-cover structure, the duration and phenology of the ice cover further influence ecological processes under-ice and post ice-off by altering mixing regimes, light and nutrient availability which can have consequences for interactions within the food web. Earlier ice-off in spring promotes wind-induced mixing which increases turbulence and reduces light availability in the water column (Adrian et al., 2009; Salonen et al., 2009). In comparison, longer ice periods allow for convective mixing beneath the ice, which circulates nutrients and keeps phytoplankton suspended in the photic zone, thereby promoting autotrophic, non-motile taxa such as diatoms (Beall et al., 2016; Jakobsson et al., 2025). Phytoplankton dynamics in relation to shifts in ice cover duration can also propagate to higher trophic levels with mismatches between phyto- and zooplankton growth in spring (Winder and Schindler, 2004).

In addition to the properties and duration of ice cover, runoff dynamics which alter organic matter inputs during ice cover can be important drivers for growth of organisms in under-ice food webs. Runoff can lead to pulses of terrestrial organic matter enriched in phosphorus, nitrogen, and dissolved organic carbon (Wilson et al., 2019; Kincaid et al., 2022; Seybold et al., 2022) entering ice-covered lakes. Such inputs stimulate bacterial growth, increasing the activity of the microbial loop and the transfer of carbon and nutrients to higher trophic levels (Berggren et al., 2010). Increased bacterial growth and terrestrial organic matter can provide an important energy source for mixotrophic phytoplankton (Hamsher et al., 2020; Socha et al., 2023) and zooplankton (Taipale et al., 2008, 2016; Berggren, Bergström and Karlsson, 2015; Harfmann et al., 2019; Wenzel et al., 2021) during periods of low light or limited primary production. Although zooplankton can supplement their diet with terrestrial organic matter and bacteria, algal-derived biomolecules, such as omega-3 fatty acids, remain critical for their reproduction and growth (Brett and Müller-Navarra, 1997; Arendt et al., 2005). During ice cover, cold temperatures reduce metabolic rates and can constrain the exploitation of distant or energetically costly food sources (Bové and Stewart, 2002; Simoncelli, Thackeray and Wain, 2019). This can influence zooplankton feeding, as motile zooplankton often migrate between habitats to optimize prey intake (Burks et al., 2002). Thus, runoff and the resulting spatial heterogeneity in resource availability during winter may influence the relative reliance of consumers on allochthonous versus autochthonous resources. In addition, winter runoff can also influence phytoplankton growth after ice-off. For example, earlier snowmelt has been linked to reduced summer chlorophyll *a* concentrations (Hrycik et al., 2021).

Taken together, the structure and phenology of the ice cover, in combination with runoff entering ice-covered lakes can strongly influence light and nutrient dynamics which can regulate the growth of bacteria, phytoplankton and zooplankton. Importantly, processes occurring during ice cover are not isolated from the rest of the year but can set the stage for the productivity and trophic structure of the open-water season. Despite the interconnection between the ice-covered period and other seasons, there is still a large knowledge gap on what drives growth across trophic levels in under-ice food webs and how these food webs will respond to global warming.

Lake food webs under changing winter conditions

Climate-driven changes are rapidly altering both the quality and stability of lake ice across northern regions. Increasing freeze-thaw cycles and winter precipitation promote the formation of white ice, which has high air content, low bearing strength, and low transparency (Weyhenmeyer et al., 2022). Such conditions reduce light penetration and modify under-ice ecological processes (Hampton et al., 2017; Culpepper et al., 2024). For example, reduced light availability can limit phytoplankton growth and shift communities toward motile and mixotrophic taxa adapted to low-light environments (Socha et al., 2023; Jakobsson et al., 2025). Ice phenology is also changing rapidly, with many lakes freezing later and thawing earlier, leading to shorter ice-cover duration (Sharma et al., 2016). Earlier ice-off has been shown to advance spring mixing and phytoplankton blooms, which can lead to mismatches between phytoplankton and zooplankton growth (Winder and Schindler, 2004; Sommer et al., 2012). At the same time, global changes in temperature and precipitation are modifying runoff and nutrient regimes (Huntington, 2006; Pierson et al., 2013; Hrycik et al., 2024). Increased rainfall and greater snowmelt volumes have been linked to lower phytoplankton growth after ice-off (Hrycik et al. 2024), while enhanced terrestrial organic matter and nutrient inputs (Wilson et al., 2019; Seybold et al., 2022) can stimulate bacterial and mixotrophic production under low-light conditions (Kritzberg et al., 2004; Berggren et al., 2010; Hamsher et al., 2020; Socha et al., 2023). Despite these observations, the combined effects of changing ice phenology, ice quality, and winter runoff remain poorly understood. In particular, it is unclear how concurrent shifts in light regimes and nutrient dynamics during winter will affect the growth and quality of basal resources available to zooplankton and the seasonal coupling between primary producers and consumers. Addressing these gaps is essential for predicting how continued climate change will alter the functioning and resilience of northern lake ecosystems.

Aims of the thesis

The overarching aim of the thesis is to advance our understand of how changing winter and ice-cover conditions influence the structure and functioning of lake food webs. Traditionally, ice-covered lakes have been viewed as biologically dormant, with low primary productivity and metabolic activity. However, recent observations increasingly challenge this assumption, suggesting that winter represents a dynamic period with important consequences for the seasonal development of plankton communities. In this thesis, two factors that are currently undergoing change in northern regions are of focus, 1) the duration and structure of lake ice and 2) the timing and magnitude of runoff entering ice-covered lakes. These factors influence the availability of light and nutrients, mixing dynamics and habitat connectivity under ice. By integrating long-term observational data, a controlled experiment and comparative cross-lake analyses, the importance of these factors in shaping winter food webs are explored.

The specific aims of the thesis (Fig. 2) are to:

- Understand the effects of ice cover duration and ice quality on phytoplankton growth and composition (paper I-II)
- Investigate the role of runoff events, and specifically the input of nutrients and terrestrial organic matter, in structuring under-ice lake resources and consequent food-web interactions (paper III-IV)
- Identify food-web interactions and food quality dynamics below ice (paper I, III-IV) and spatially across lake habitats (paper IV)

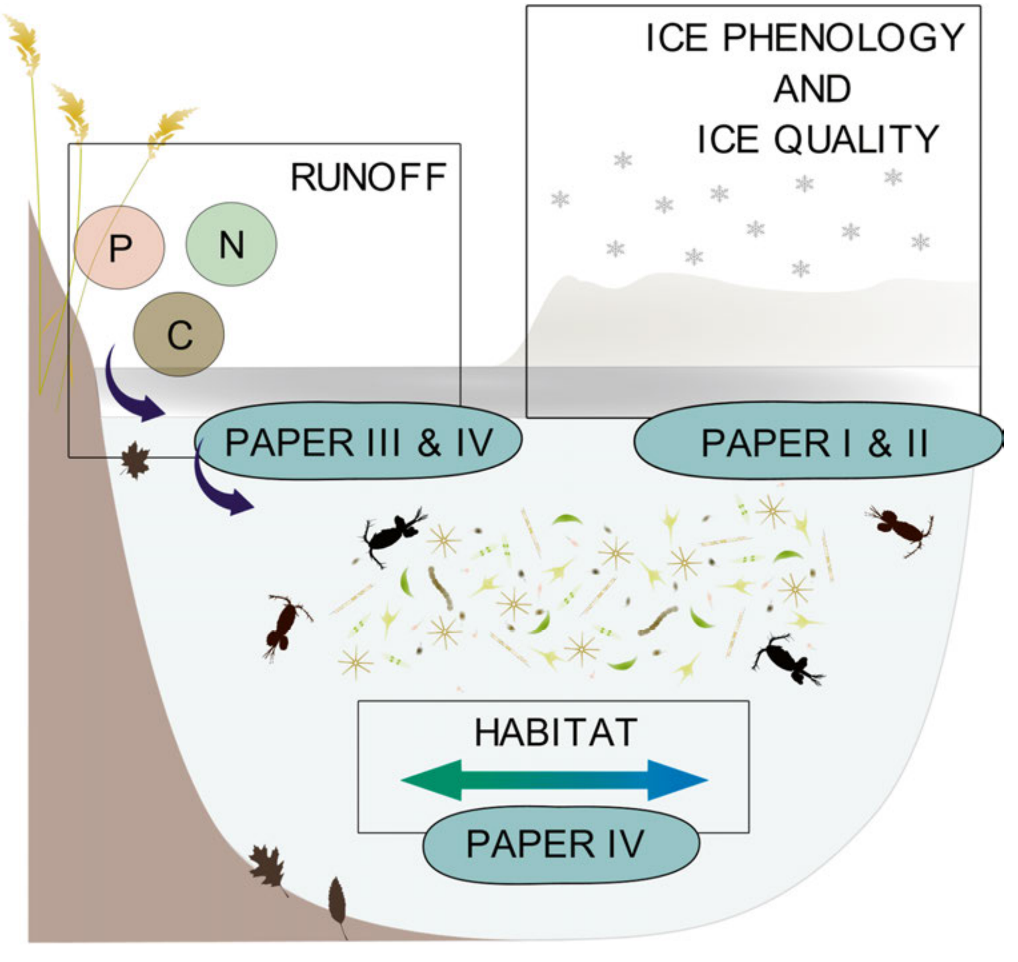

Figure 2. The specific aims of the thesis highlighted in separate boxes, and the respective paper related to the specific aim.

Material and Methods

Study design

Theoretical approach

To better understand how ice quality and snow cover affects under-ice food webs, a conceptual review of current knowledge on lake processes under differing ice quality conditions was performed (paper I). Specifically, existing data on ice thickness, ice quality (black and white ice), snow depth, and phytoplankton composition and chlorophyll *a* (chl-*a*) from the literature were synthesized to provide conceptual context for the empirical studies that follow.

Study sites

Two of the studies comprising this thesis (paper II-III) were performed in Erken, a mesotrophic lake in central Sweden (Fig. 3). The lake provides an important basis for studying changes in ice cover regimes as it has been continuously monitored for ice phenology and lake chemistry since the 1940's. In addition, to assess how terrestrial organic matter availability, serving as a proxy for runoff, influences under-ice food webs, six lakes spanning a gradient of terrestrial organic matter estimated from specific UV absorbance (SUVA; Weishaar et al. 2003) were selected for a field sampling campaign (paper IV). The lakes are situated in Uppland, central Sweden (Fig. 3) and vary in nutrients and morphology, in addition to SUVA (see paper IV for further details).

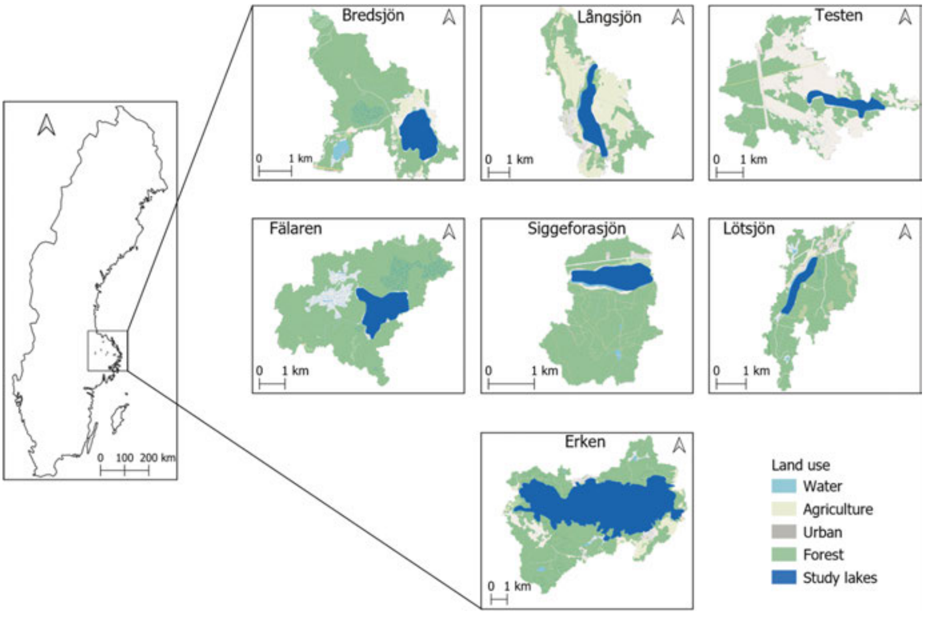

Figure 3. Location of the seven study lakes (paper II-IV) in Sweden, as well as their catchment area and land-use cover.

Field sampling

A field sampling campaign was performed to investigate how differences in resource availability and use shape food webs during winter and spring (paper IV). For the campaign, six lakes in central Sweden (Fig. 3) were sampled approximately bi-weekly during the ice-covered period (Jan-April) and monthly after ice-off (May). Samples for fatty acid (FA) analysis of copepods and seston (20-120 µm) were collected in the shoreline (littoral) and open water (pelagic) habitat of each lake to estimate the spatial heterogeneity in resource availability and assimilation. The phytoplankton community composition in each habitat was also determined.

In addition to the field sampling campaign, long-term monitoring data ranging from bi-weekly to monthly field measurements in Erken were used to assess phytoplankton responses to ice phenology and snow cover (paper II) using data on ice phenology, phytoplankton composition and chl-*a* concentrations. This data was further supplemented with snow depth data from the Swedish Hydrological and Metrological Institute (SMHI) for the same years. Snow depth was measured manually at stations nearby the lake and were used as a proxy for snow cover on the lake (paper II).

Mesocosm experiment

To understand the interacting effects of light and nutrients on the structure of under-ice food webs, particularly via the timing of runoff events, we conducted a mesocosm experiment in Erken (paper III). A mesocosm experiment uses contained experimental units deployed in-situ and can be useful when controlled manipulations of environmental variables are wanted to simulate natural conditions while maintaining replicability and minimizing external variability. In our experiment, this approach was used to address effects of nutrient pulses as specific drivers during ice cover, which are otherwise challenging to study in-situ during winter. We added inorganic nitrogen (N) and phosphorus (P) at two occasions during ice cover to mimic an early and a late runoff event. Each treatment was replicated four times and samples were collected approximately every fourth day between February-April 2023. The samples were used to determine bacterial abundance, phytoplankton chl-*a*, light-response curves and community composition, and zooplankton abundance and composition. We also continuously monitored dissolved oxygen (DO), temperature and photosynthetically active radiation (PAR) in-situ. Sensors were deployed in each mesocosm and measurements were taken at 10-minute intervals.

Measurements

Bacterial cell abundance

To determine the abundance of bacterial cells in collected samples, laser scattering using flow cytometry (Gasol and Giorgio, 2000) was applied (paper III). Briefly, the cells were stained with a fluorescent marker and passed through a flow cytometer, where lasers of different wavelengths (405 and 488 nm) excite the stained cells, allowing cells to be counted at a constant flow rate.

Phytoplankton biomass

Chl-*a* concentrations were quantified and used as a proxy for phytoplankton biomass to capture short-term temporal variations (paper II-IV). Chl-*a* pigment detection in phytoplankton is a common and fast method for estimating phytoplankton biomass (Bidigare, Heukelem and Trees, 2005). The method uses extraction of chl-*a* pigments from the cells with ethanol, followed by spectrophotometric estimates of pigment concentration by measuring the absorbance at a fixed wavelength (Jespersen and Christoffersen, 1987).

Phyto- and zooplankton communities

To assess community composition shifts in phyto- and zooplankton over time (paper II-IV), we identified, counted and measured individuals of these organism groups with an inverted light microscope using the Utermöhl method (Utermöhl, 1931). Samples were sedimented in volumetric chambers and counted across the chamber bottom. Biovolumes of phytoplankton were calculated from standard geometric volume formulas (Hillebrand et al., 1999). Phytoplankton were identified to genus level and zooplankton to order level. Although microscopy counts and measurements are more labour-intensive than pigment-based detection, they offer valuable detail on taxonomic composition. This taxonomic information can serve as a rough proxy for functional groups and was used here to classify phytoplankton trophic modes (autotrophic or mixotrophic; paper II-IV).

Estimating trophic interactions

To estimate the assimilation of different resources by copepods we applied FA analysis (paper IV). We analyzed the FA composition of copepods and seston during winter and spring to track the assimilation of specific resources such as phytoplankton, bacteria, and terrestrial organic matter during the ice-covered period. Briefly, lipids were extracted from samples using organic solvents, purified, and methylated for analysis by gas chromatography-mass spectrometry (GC-MS). Specific FA compounds were identified by comparing retention times with known standards. The identified compounds were then grouped into biomarker categories. Long-chained saturated FAs (SAFAs;18:0-24:0) were used as generic markers of detrital or terrestrial organic matter (Boschker, Kromkamp and Middelburg, 2005). The three PUFAs arachidonic acid (ARA; 20:4n6), eicosapentaenoic acid (EPA; 20:5n3), and docosahexaenoic acid (DHA; 22:6n3) were used to assess nutritional quality (PUFAs) and together with the monounsaturated FA 24:1n9, these were also used as algal biomarkers typical for many phytoplankton groups such as diatoms, cryptophytes, chrysophytes, and dinophytes (Brett and Müller-Navarra, 1997; Taipale et al., 2013; Grosbois et al., 2017). Bacterial FAs commonly include branched, odd-chained, and cyclic FAs (Parker et al., 1982; Haubert et al., 2006; Grosbois et al., 2017), and in our study, branched, hydroxy, and cyclic FAs were used as bacterial biomarkers. As FAs are metabolically stable and accumulate in the consumer tissue, they can be used to trace an organism's diet and by this, assess trophic interactions (Napolitano, 1999).

Data analysis and visualization

Data were analyzed using a combination of univariate and multivariate statistical approaches. Long-term trends in ice thickness, ice phenology and ice quality (black ice/white ice ratio) were visualized using whisker boxplots (paper I). The same approach was used to visualize ecological effects of changing ice- and snow conditions, including phytoplankton chl-*a* responses to snow cover removal (paper I).

Further, long-term monitoring data over two decades were used to evaluate phytoplankton responses to ice phenology and snow cover (paper II). Canonical correlation analysis (CCA) was used to analyze and visualize compositional shifts in phytoplankton in relation to ice phenology and snow depth. CCA was chosen as a constrained option for our non-linear (axis length > 4, ter Braak and Prentice 1988) multivariate data (paper II). Linear and binomial regression models were used to identify absolute and relative shifts, respectively, in phytoplankton trophic mode (mixotrophic vs. autotrophic, paper II). Finally, linear regression models were used to analyze phytoplankton chl-*a* in relation to snow depth during ice cover in winter (Jan-Mar, paper II).

In addition, generalized additive mixed effect models (GAMMs) were used to analyze how bacteria, phytoplankton and zooplankton responded to altered timing of nutrient additions under ice (paper III). The phytoplankton community was divided into mixo- and autotrophic taxa and their responses to nutrient addition timing were analyzed separately (paper III). GAMMs were selected based on their flexibility to model non-linear patters while controlling for covariates (Wood, 2017). DO, which we used as a proxy for primary production, was further analyzed using a linear mixed-effect model (LME) to test whether DO responded to nutrient addition timing (paper III).

Further, fatty acid composition of seston and copepods from six study lakes were analyzed using partial redundancy analysis (pRDA, paper IV). pRDA was chosen as a constrained option for our linear (axis length < 3, ter Braak and Prentice 1988) multivariate data, with the ability to control for repeated measurements using conditioning variables (Oksanen et al., 2022). With pRDA, the relationship between seston fatty acid composition with phytoplankton community composition at class level and habitat was tested to identify the importance of phytoplankton compositional shifts and habitat in explaining seston fatty acid variation (paper IV). Additionally, the relationship between copepod fatty acid composition with seston fatty acid composition and habitat was tested to identify whether fatty acid variation in seston, and habitat predicted copepod fatty acid variation (paper IV). In addition, we used LME to determine potential differences in the concentration of essential

PUFAs between habitats and lakes in both seston and copepod FAs. The concentration of the three PUFAs EPA, DHA and ARA were summed to represent essential PUFAs (paper IV). Finally, the relationships between essential PUFAs in seston and copepods, and SUVA were tested by fitting two quadratic regression models using an LME model for seston and a standard linear model for copepods because the random factor in the copepod LME model explained negligible variation (paper IV).

Results and Discussion

Food webs in relation to ice cover

Climate-driven changes in both the duration and composition of ice cover, together with shifts in runoff timing and magnitude, are reshaping under-ice habitats. Along with shorter ice periods, later freeze-up, and earlier breakup, ice conditions are shifting from transparent black ice to more opaque white ice (paper I). Together, these changes alter light transmission and mixing beneath the ice and post ice-off (paper I), and change nutrient regimes, thereby controlling two of the main drivers of food-web interactions. Under the ice, organisms in the food web remain active, including bacterial mineralization, phytoplankton growth and zooplankton grazing (paper I-IV).

Although bacteria are not directly light dependent, under-ice studies show that their growth can respond to phytoplankton-derived organic matter (paper I), while also occurring independently when other nutrient sources are available (paper III). Thus, changes in light following an ice cover are likely not directly driving bacterial growth, but can mediate it through effects on phytoplankton. Importantly, this suggests that bacteria respond primarily to DOM availability, as observed elsewhere (Tulonen et al., 1994), and play a central role in nutrient recycling within under-ice food webs. These observations were further supported by an experimental manipulation of nutrients under ice, resulting in increased bacterial abundances where nutrients were added (Fig. 4a, paper III). Bacteria also constitute an important resource for higher trophic levels during ice cover, as reflected by their contribution to the fatty acid composition of seston and copepods (paper IV). Taken together, these results demonstrate that bacteria form a key link between nutrients and organic matter inputs, and higher trophic levels during ice cover. Their growth can be directly stimulated by DOM inputs or indirectly linked to light-driven phytoplankton production, suggesting that changes to light and especially DOM regimes under ice alter bacterial pathways in ice-covered lakes.

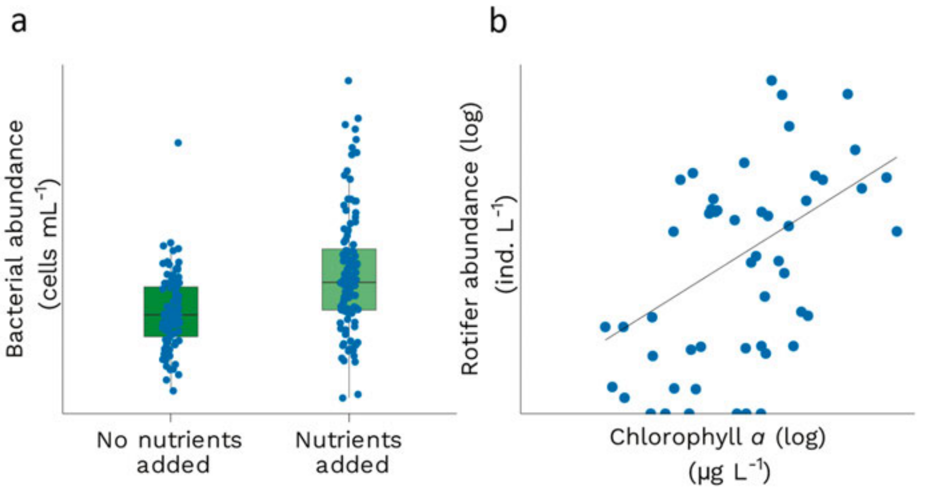

Figure 4. a) Bacterial abundance (cells mL^{-1}) under conditions without and with nutrients added below ice cover, based on data presented in paper III and b) log-transformed rotifer abundance (ind. L^{-1}) in relation to log-transformed phytoplankton chlorophyll *a* concentration (µg L^{-1}), based on data presented in paper III.

In comparison to bacteria, phytoplankton are commonly light limited (paper I-III), with growth conditions determined by the ice cover duration, ice composition and the presence of snow (paper I-II). The duration of ice cover changes light and mixing conditions after ice-off which alters phytoplankton growth and composition (paper I-II). Specifically, longer ice periods and later ice-off increased phytoplankton chl-*a* concentrations after ice-off and promoted a diverse phytoplankton community including diatoms, mixotrophs and green algae (paper II). In contrast, delayed ice-on dates were associated with fewer taxa, mainly dominated by cyanobacteria and certain diatoms (paper II). These increases in phytoplankton growth and diversity with longer ice periods likely reflect a combination of nutrient recirculation through convective mixing and reduced turbidity compared to ice-free conditions (Zepernick et al., 2024). In addition to ice phenology, the structure of the ice cover and presence of snow cover are main regulators of under ice light conditions (Bolsenga and Vanderploeg, 1992) with consequent effects on phytoplankton growth and composition (paper I-II). Under black-ice conditions, phytoplankton biomass is often higher and mainly composed of non-motile taxa, for example diatoms, due to higher light availability and convective mixing (paper I). In contrast, white ice and snow cover reduce light penetration and mixing, favouring motile and mixotrophic taxa such as cryptophytes, chrysophytes or dinoflagellates (paper I). Experimental snow-removal studies confirmed that clearer ice conditions enhance phytoplankton chl-*a* concentrations (Fig. 5a, paper I).

These reported observations (paper I) were further supported by long-term data from Erken (paper II). Phytoplankton chl-*a* concentrations decreased with increasing snow depth (Fig. 5b; Paper II), further highlighting the importance of light availability for phytoplankton growth during ice cover. The phytoplankton community generally shifted towards a dominance of mixotrophs with increasing snow depth (paper II), supporting the idea that mixotrophs have an advantage over light-dependent taxa under low-light conditions (Rothhaupt, 1996). Overall, these results demonstrate that ice duration, ice quality and snow cover regulate light availability with effects on both the magnitude and functional structure of phytoplankton communities below ice and after ice-off. These factors not only determine the extent of phytoplankton growth but also influence the quality and timing of resources available to higher trophic levels, as phytoplankton differ in their nutritional quality, with diatoms generally considered higher-quality food for zooplankton than many mixotrophic taxa (Jónasdóttir, 2019; Taipale, Peltomaa and Salmi, 2020).

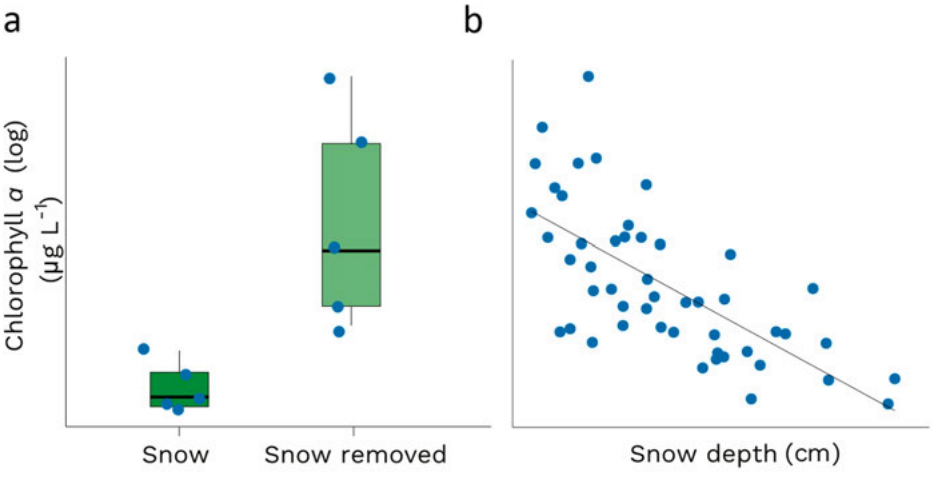

Figure 5. a) Log-transformed chlorophyll *a* concentrations (μg L^{-1}) under experimentally removed snow-free, and snow-covered conditions, adapted from paper I, and b) log-transformed chlorophyll *a* concentrations (μg L^{-1}) along a snow depth gradient (cm), based on data presented in paper II. *Panel a) adapted from Culpepper et al., 2024.*

Zooplankton also constitute an important part of under-ice food webs, especially through grazing and predation, and therefore, their growth can be directly linked to shifts in available resources (paper I, III-IV). Zooplankton can track phytoplankton responses to light, with higher abundances under low- or snow-free conditions (paper I). Similarly, increases in rotifers can be driven by increases in phytoplankton chl-*a* concentrations under ice (Fig. 4b; paper

III), indicating that resource availability can be transferred to higher trophic levels even during ice cover. Increases in rotifers were accompanied by higher copepod abundances, likely reflecting enhanced prey availability (paper III). These findings were further supported by field observations where shifts in resource quality and composition were mirrored in zooplankton communities (paper IV). Together, these results demonstrate that bottom-up and top-down controls are occuring below ice, with zooplankton actively linking lower and higher trophic levels through resource assimilation.

Runoff effects on food webs under ice

In addition to light availability below ice, runoff timing and magnitude were identified as important drivers of under-ice food web structure (paper III-IV). Specifically, the timing of nutrient additions, which was used as a proxy for runoff timing, affected growth of phytoplankton and zooplankton, while bacteria retained the same abundances independent of nutrient addition timing (paper III). When nutrients became available earlier during the ice-covered period, growth of mixotrophic phytoplankton was promoted (Fig. 6a). The higher mixotrophic biovolumes observed when nutrients were available earlier likely reflect reduced competition with light-dependent taxa (Rothhaupt, 1996) and a strengthening of the heterotrophic pathway within the food web. In contrast, late nutrient additions caused a stronger phytoplankton spring bloom compared to the early runoff scenario (Fig. 6b). These shifts in phytoplankton resources were mirrored at higher trophic levels, where rotifer abundances marginally decreased with late nutrient additions, and generally decreased when nutrients were added (paper III). Increased predation pressure related to the higher copepod abundances observed in the nutrient addition treatments, could explain the reduction in microzooplankton (Brandl, 2005; Bundy et al., 2005) and suggest that the system shifted from bottom-up to top-down control following nutrient additions. The observed structural changes in the food web following earlier nutrient availability likely resulted in lower bioavailability of nutrients for phytoplankton in spring when light increased, resulting in a comparably lower spring bloom. Thus, while light remains a key regulator of phytoplankton growth and subsequent trophic interactions (paper I-III), late runoff can enhance nutrient concentrations, promoting phytoplankton blooms when light conditions are sufficient. Overall, these findings suggest that earlier runoff during ice cover can shift the food web towards a heterotrophic pathway via increased mixotrophy and reduce bioavailability of nutrients with consequences for the phytoplankton spring bloom.

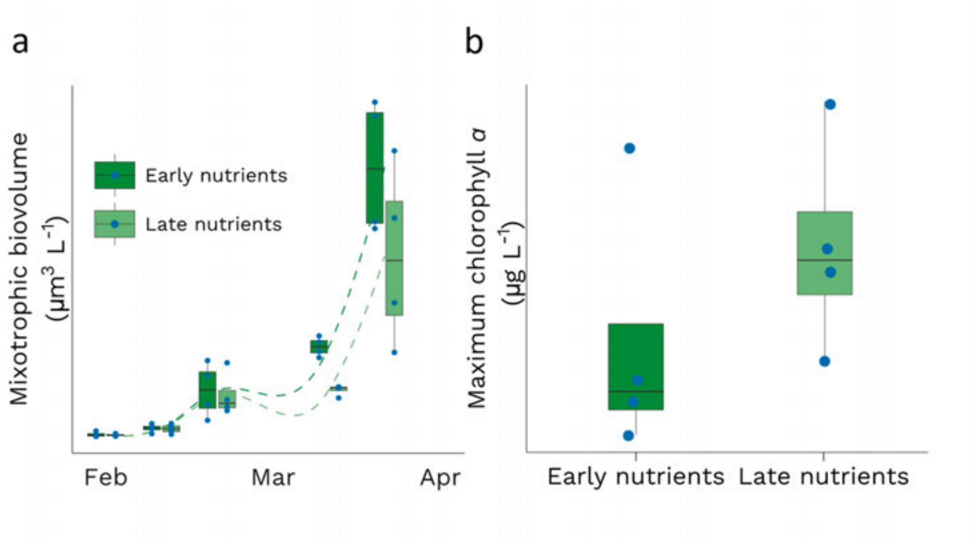

Figure 6. a) Changes in the biovolume of mixotrophs (µm^3 L^{-1}) over time in relation to early and late nutrient additions based on data presented in paper III, and b) maximum phytoplankton chlorophyll *a* concentrations (µg L^{-1}) observed during the experiment in paper III in relation to early and late nutrient additions.

Field observations further supported the experimental observations that runoff can be important in structuring under-ice food webs (paper IV). Runoff magnitude, approximated by terrestrial organic matter availability and indicated by SUVA, was negatively related to resource nutritional quality (PUFA proportions) at high SUVA levels during ice cover (paper IV). The terrestrial signal in resources was only partly reflected in copepods, where copepods in lakes rich in terrestrial inputs displayed higher proportions of bacterial and terrestrially derived biomarkers, but their nutritional quality (PUFA proportions) remained constant at high levels of terrestrially derived DOM (paper IV). Copepods are generally selective feeders and can detect and preferentially assimilate phytoplankton (DeMott, 1989). It is therefore possible that, despite an increased abundance of terrestrial resources, copepods selectively assimilated high-quality phytoplankton, maintaining their nutritional quality rather than showing a decline which would be expected if terrestrial resource acquisition would dominate (Hixson et al. 2015; paper IV). It is also possible that copepods were selectively retaining PUFAs for reproduction (Arendt et al., 2005) or survival during low temperatures (Hartwich, Martin-Creuzburg and Wacker, 2013; Grosbois et al., 2017). Overall, these findings imply that lakes receiving substantial terrestrial inputs likely support a partially heterotrophic food web during winter, as shown by enrichment of bacterial and terrestrial fatty acids in both seston and copepods. However, copepods appear to be selectively retaining or assimilating PUFAs, maintaining their nutritional quality even when overall resource quality declines (paper IV).

Taken together, these results highlight that increased runoff (paper IV), and particularly nutrient inputs associated with it (paper III), can strengthen heterotrophic pathways in lake food webs. These inputs stimulate bacterial growth and favour mixotrophic phytoplankton under low-light conditions. However, the timing of runoff events can determine the extent of heterotrophic reliance and the nutritional quality of under-ice communities.

Spatial heterogeneity in under-ice food webs

The growth of organisms in under-ice food webs was found to be driven by both light, nutrients and organic matter availability related to ice cover and runoff (paper I-IV), but how food webs vary spatially across lakes which receive different amounts of terrestrial inputs remained unclear. Field observations showed clear heterogeneity in resource availability and structure of under-ice food webs (paper IV). Resource and consumer nutritional quality (PUFA proportions) differed across lake habitats. Specifically, seston and copepods in pelagic habitats showed higher proportions of algal-derived PUFAs (Fig. 7), while littoral seston and copepods instead were enriched in bacterial and terrestrial biomarkers (paper IV).

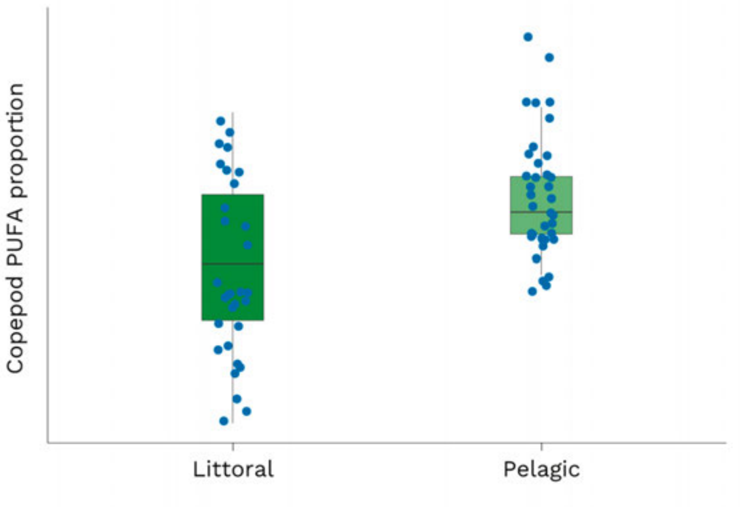

Figure 7. Proportion of copepod PUFAs (EPA, DHA and ARA) in littoral and pelagic habitats based on data presented in paper IV.

Phytoplankton generally contain higher concentrations of these long-chained PUFAs and are thus considered higher-quality food compared to terrestrial and bacterial resources (Napolitano, 1999; Hixson et al., 2015), but their quality can be taxa-dependent (Brett and Müller-Navarra, 1997; Taipale, Peltomaa and Salmi, 2020). The observations suggest that copepods were obtaining PUFAs from feeding on high-quality phytoplankton taxa in the pelagic habitat rather than reflecting higher total phytoplankton availability, as phytoplankton biovolumes did not differ between habitats (paper IV). Multivariate analyses further revealed that littoral habitats were associated with several hetero- or mixotrophic phytoplankton, such as ciliates, cryptophytes and euglenids, whereas pelagic habitats were characterized by chrysophytes and chlorophytes. The relatively higher availability of PUFA-rich chrysophytes in the pelagic habitat, together with the dominance of lower-quality hetero- and mixotrophic taxa in the littoral habitat, may explain the observed habitat differences in copepod PUFA proportions. Although cryptophytes and diatoms, also present in the littoral habitat, are typically rich in essential PUFAs (Brett and Müller-Navarra, 1997; Jónasdóttir, 2019; Taipale, Peltomaa and Salmi, 2020), their influence may have been reduced by the overall dominance of lower-quality mixo- and heterotrophs in the littoral habitat. Together, these results indicate that spatial heterogeneity in resource quality is transferred to higher trophic levels, with copepods in littoral habitats exhibiting lower nutritional quality. This pattern likely reflects a more heterotrophic energetic pathway in the littoral habitat, driven by terrestrial inputs that stimulate bacterial production and increase the abundance of hetero- and mixotrophic plankton.

Broader implications and future perspectives

Lakes at northern latitudes are undergoing profound transformations driven by global warming. Beyond the well-documented shortening of ice-cover duration (Sharma et al., 2016), recent research, including this thesis, highlights a change in the composition of the ice cover and snow depth as critical drivers of under-ice food-web interactions (paper I-II). Increasing freeze-thaw cycles and rain-on-snow events following warmer winters (Bintanja and Andry, 2017) promote the formation of white ice (paper I) and can change the timing and magnitude of runoff to ice-covered lakes (Hrycik et al., 2021, 2024; Seybold et al., 2022). The increasing prevalence of white ice is likely to reduce under-ice light availability (paper I), although total snow cover is projected to decrease at northern latitudes (Bintanja and Andry, 2017). The combined results of this thesis suggest that at latitudes where ice-cover duration is shortening, concurrent changes in winter precipitation, runoff timing and ice quality will strongly affect under-ice food webs by altering light and nutrient regimes. Specifically, such reduction in light and increases in nutrients and terrestrial organic matter can limit phytoplankton growth and shift the energy base of the food web toward mixotrophic and heterotrophic pathways (paper I-IV). Similarly, greater heterotrophy following earlier or higher runoff and lower light availability can reduce trophic transfer efficiency, as respiratory losses increase relative to reproduction or biomass gains following decreases in resource nutritional quality (Weers and Gulati, 1997; Darchambeau, Faerovig and Hessen, 2003; Bednarska, 2022). Although consumers may buffer this reduction in nutritional quality through selective retention or feeding (paper IV), reliance on low-quality resources could ultimately constrain growth and elevate metabolic costs across trophic levels. Thus, over time, shifts in nutritional quality could negatively affect zooplankton growth and reproduction, and consequently reduce fish recruitment after ice-off (Fig. 8). Future efforts should aim to incorporate higher trophic levels when assessing how changes in resource quality propagate through under-ice food webs.

In addition, increased reliance on heterotrophic and mixotrophic production could alter biogeochemical cycling in northern lakes. As warming enhances winter runoff and terrestrial inputs, mixo- and heterotrophic mineralization will likely play an expanding role in lake carbon dynamics, especially during winter (paper III-IV). Such shifts have the potential to increase CO_2 fluxes, as respiratory losses rise when trophic transfer efficiency declines (Weers and Gulati, 1997; Darchambeau, Faerovig and Hessen, 2003; Bednarska, 2022) and carbon fixation through primary production is hampered (Fig. 8). Future efforts should aim to link under-ice microbial processes with biogeochemical models to better predict how changing ice regimes will influence biogeochemical cycling of lakes during and post ice-off.

In brief, future studies should aim to:

- Couple ecological and biogeochemical measurements to quantify the role of bacteria, mixotrophs, and heterotrophs in winter carbon cycling.
- Incorporate higher trophic levels to examine how changes in resource quality propagate through under-ice food webs.
- Expand the temporal scope to link under-ice processes to those occurring prior to, and post ice-off.
- Apply molecular approaches to more accurately identify active functional traits to better predict energy transfer within the food web.
- Simultaneously quantify the effects of shifting ice phenology, ice quality and runoff regimes on biogeochemical cycling and trophic transfer.

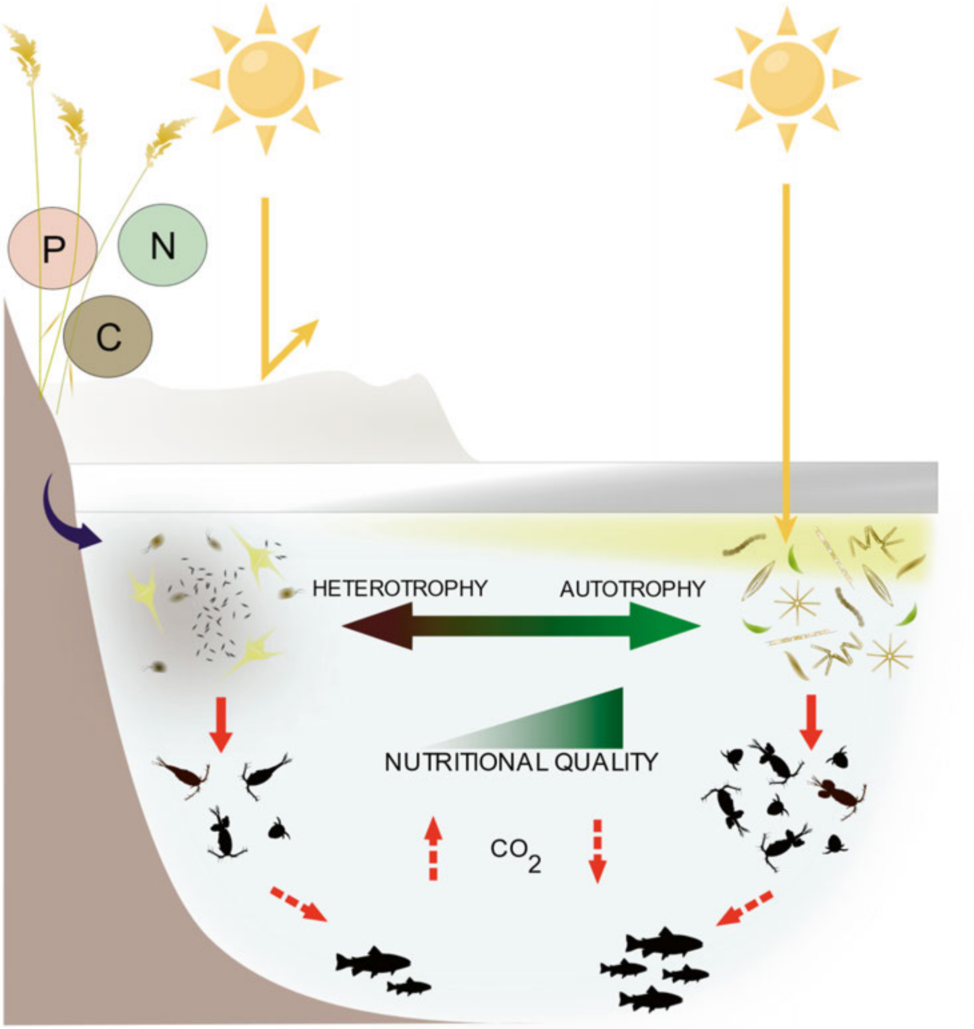

Figure 8. Conceptual overview of how ice quality, snow cover and runoff (C, N, P) affect lake hetero- or autotrophy, nutritional quality and growth across trophic levels in an under-ice food web. Direct observations from this thesis are marked in solid red arrows, while indirect implications of these observations are marked in dashed red arrows.

Conclusions

The overarching conclusion of this thesis is that organisms in food webs in ice-covered lakes remain active, challenging the traditional view of winter dormancy. Light, nutrients and organic matter availability following shifts in ice quality and phenology, and runoff regimes act as main drivers of carbon pathways in ice-covered lakes, regulating relative heterotrophy in food webs below ice. The main conclusions are listed below.

Ice-cover effects on lake food webs

- Ice quality, in particular the relative amounts of black and white ice, together with snow cover, controls light transmission and thereby the balance between autotrophy, mixotrophy, and heterotrophy in under-ice food webs. Specifically, clear ice conditions were found to support autotrophic taxa such as diatoms while light limitation under snow cover increased the importance of mixotrophs, which can act as a functional buffer of productivity and nutrient cycling when autotrophic production is diminished. However, because diatoms generally are of higher nutritional quality than many mixotrophic taxa, light limitation and the associated shift in community composition have the potential to reduce resource quality for grazers, ultimately constraining zooplankton growth and potentially reducing the success of fish recruitment.
- The duration of ice cover regulates light, mixing, and nutrient dynamics following ice-off, which are important in shaping spring food webs. Longer ice periods increased the magnitude of the phytoplankton spring bloom and promoted a diverse phytoplankton community, indicating that changes in ice duration can determine resource quantity and quality available for higher trophic levels in spring. In particular, delayed ice-on and earlier ice-off negatively affected a majority of the phytoplankton community while few taxa, including lower-quality cyanobacteria, were positively associated with such conditions. Alterations in phytoplankton quantity and diversity could propagate to zooplankton reproduction and growth. Specifically, the presence of high-quality taxa could allow for selective feeding, while a

dominance of low-quality taxa instead has the potential to decrease trophic transfer efficiency in the food web.

The role of runoff in structuring under-ice food webs

- The timing of runoff, and specifically inorganic nutrient availability, during ice cover is an important determinant of under-ice food-web structure. An early runoff scenario below ice supported mixotrophic phytoplankton, whereas late runoff promoted higher total phytoplankton biomass during the spring bloom. These findings suggest that the timing of runoff, for example following snowmelt, can regulate the relative contribution of autotrophy to heterotrophy in lake food webs.
- High amounts of terrestrially derived organic matter reduced nutritional quality of basal resources, which was only partly mirrored in consumers, suggesting that selective retention of high-quality resources or feeding on high-quality phytoplankton can partly compensate expected nutritional losses following increased terrestrial inputs linked to runoff regimes. However, assimilation of low-quality resources in consumers could eventually lead to increased metabolic costs to meet their nutritional demands.
- Altogether, the findings of this thesis suggest that increased runoff, and especially early during the ice cover period, can increase heterotrophic reliance in the food web through hetero- and mixotrophic pathways leading to a decline in nutritional quality. Such a decline in the nutritional quality of basal resources could reduce trophic transfer efficiency in the food web and increase metabolic costs and respiratory processes relative to primary production.

Spatial heterogeneity in food webs below ice

- Under-ice food webs differ in nutritional quality and structure spatially across lake habitats. Specifically, littoral habitats were enriched in terrestrial and bacterial fatty acids in both resources and consumers which resulted in lower nutritional quality of these, suggesting that terrestrial subsidy in littoral food webs increases their heterotrophic reliance under ice. In contrast, pelagic habitats displayed higher nutritional quality and algal enrichment. Overall, our results highlight that under-ice food webs are spatially decoupled, likely due to variation in resource input combined with low temperatures that constrain metabolic activity and the assimilation of spatially distant resources.

Populärvetenskaplig Sammanfattning

Sjöar är dynamiska ekosystem som binder samman land och vatten, och deras näringsvävar styrs av flödet av energi och näringsämnen mellan olika organismer. Energin som driver näringsväven kommer från två huvudsakliga källor vilka är produktionen inom sjön, till exempel genom växtplankton och makrofyter, samt genom material som tillförs från omkringliggande landekosystem. Växtplankton, mikroskopiska alger som lever i vattnet, spelar en särskilt viktig roll eftersom de omvandlar solljus och näringsämnen till organiskt kol genom fotosyntesen. Detta kol utgör grunden för högre trofiska nivåer som djurplankton och fisk. Två av de viktigaste faktorerna som styr växtplanktons tillväxt är ljus och näringsämnen. Ljuset tillför energi till fotosyntesen, medan näringsämnen som fosfor och kväve fungerar som byggstenar för deras celltillväxt. Under vintern täcks många sjöar på norra halvklotet av is och snö, vilket kraftigt minskar både ljus och temperatur. På grund av dessa förhållanden har istäckta sjöar länge ansetts vara biologiskt inaktiva, med liten eller ingen tillväxt av organismer förrän våren kommer. Nyare forskning har dock utmanat detta synsätt och visat att ekosystem under isen kan vara förvånansvärt aktiva. Hur aktiva dessa ekosystem är beror till stor del på hur mycket ljus som kan tränga igenom isen. Om isen är klar och snötäcket är tunt eller saknas helt, når tillräckligt med ljus vattnet för att fotosyntesen ska kunna fortgå och växtplankton växa. Om snö däremot ansamlas på isen, eller om isen blir vit och ogenomskinlig på grund av luftbubblor, minskar ljusinsläppet och växtplanktonproduktionen avtar. Både hur länge sjöar är istäckta och sammansättningen av istäcket spelar därför en viktig roll för produktiviteten under vintern. Utöver ljusinsläpp genom isen är även näringsämnen som tillförs sjön under istäcket en annan viktig faktor. Tillrinning från omgivande landområden kan transportera organiskt material och näringsämnen som fosfor och kväve till sjöar. Traditionellt har det antagits att dessa näringsämnen förblir outnyttjade tills våren, när ljusförhållandena förbättras. Det är dock numera tydligt att organismer förblir aktiva under isen och kan reagera på förändringar i både ljus och näringshalter innan islossningen. Trots detta har tidigare studier främst fokuserat på processer som sker efter islossningen, medan kunskap om hur näringsvävar fungerar under isen har varit begränsad. Denna avhandling undersöker därför samspelet mellan bakterier, växtplankton och djurplankton under istäcket och vad som styr deras aktivitet under vintern. För att fylla denna kunskapslucka kombinerades data från tidigare studier och från sjön Erkens miljöövervakningsprogram (artikel I-II) med ett kontrollerat experiment i sjön Erken (artikel III) samt en fältstudie i sex sjöar med olika tillförsel av organiskt material från land (artikel IV). Resultaten från de första studierna (artikel I-II) visar att snötäcket har stor betydelse för växtplanktons tillväxt under isen. Tunnare snö ökade ljusgenomsläppet och därmed växtplanktonproduktionen, medan tjockare snö eller vitis kraftigt begränsade ljuset och minskade tillväxten. Även isens varaktighet visade sig påverka produktiviteten efter islossningen. Kortare isperioder var kopplade till lägre växtplanktonproduktion på våren, troligen eftersom tidigare islossning orsakar omblandning av vattnet och grumlighet, vilket minskar ljusförhållandena för fotosyntes. Dessa resultat visar att förändringar i isens egenskaper kan påverka både tidpunkten och omfattningen av primärproduktion i sjöar. Förutom ljuset visade avhandlingen också att näring, och speciellt vid vilken tidpunkt denna tillförs, är viktig för tillväxt av organismer under vintern. I ett experiment (artikel III) manipulerades tidpunkten av näringstillförsel. Resultaten visade att växtplankton kan öka sin tillväxt under isen när näringsämnen tillförs, om ljuset är tillräckligt. När näring tillfördes sent under vintern, nära våren, ökade växtplanktonbiomassan. När näringen däremot tillfördes tidigt på vintern, under svaga ljusförhållanden, dominerades tillväxten istället av mixotrofa växtplankton, arter som både kan fotosyntetisera och ta upp organiskt material och bakterier som näring. Detta visar att planktonsamhällets sammansättning under isen beror på samspelet mellan ljus och näringsnivåer. Tidig näringstillförsel, när ljuset fortfarande är lågt, gynnar organismer med heterotrofa egenskaper, medan senare näringstillförsel vid starkare ljus gynnar totala tillväxten av växtplankton. Fältstudien över sex sjöar (artikel IV) breddade förståelsen om hur tillrinning och organiskt material från land påverkar näringsvävar under isen. Sjöar med högre halter av löst organiskt kol (DOC) från landekosystem uppvisade starkare heterotrofa drag i sina näringsvävar. Det organiska materialet stimulerade bakteriell tillväxt och ökade därmed betydelsen av den "mikrobiella loopen" för energiöverföring. Samtidigt minskade den näringsmässiga kvaliteten i sjön, eftersom bakterier och organiskt material från land saknar viktiga fleromättade fettsyror (PUFAs), exempelvis flera omega-3-fettsyror, som produceras av växtplankton. Växtplankton fortsatte att vara en viktig födokälla för djurplankton, särskilt i den öppna vattenmassan (pelagialen). I strandzonen (littoralen) var djurplankton i högre grad beroende av bakterier och material från landekosystem. Detta visar att näringsvävar under isen inte är homogena, utan varierar spatiellt mellan olika habitat beroende på exempelvis ljus, omblandning och tillförsel av organiskt material. Sammantaget visar resultaten från denna avhandling att ekosystem under isen är långt ifrån inaktiva. De styrs av ett komplext samspel mellan ljus, näringsämnen, isegenskaper och tillrinning från land. Avhandlingen visar att vinterperioden är en aktiv och ekologiskt viktig period som påverkar biologiska processer även efter islossningen. Förändringar i isens varaktighet och kvalitet kan dessutom förändra balansen mellan autotrofa, mixotrofa och heterotrofa processer i sjöars näringsvävar. Klar is och goda ljusförhållanden gynnar växtplankton med hög näringskvalitet, som kiselalger (diatoméer), medan snö och vitis gynnar mixotrofer som kan upprätthålla viss produktion men producerar föda av lägre näringsvärde. Dessa förändringar kan sprida sig uppåt i näringsväven och påverka djurplanktons tillväxt, fiskrekrytering och sjöns kol- och näringsomsättning. Resultaten är särskilt viktiga i ett perspektiv av klimatförändringar. Vintrarna blir allt varmare, och många sjöar i norra hemisfären uppvisar nu kortare och mer instabila isperioder, fler dagar med temperaturer över noll grader (töcykler), samt ökad bildning av vitis. Samtidigt väntas mer nederbörd och regn som faller på snötäcket och tinar detta att öka tillrinningen till sjöar under vintern. Dessa förändringar kan minska ljusförhållandena under isen, men också tillföra mer näring tidigt på vintern. Kombinationen av mindre ljus och mer näring kan leda till att sjöars näringsvävar under vintern skiftar mot ökad heterotrofi, vilket i sin tur minskar näringskvaliteten hos konsumenterna i sjöar. På längre sikt kan detta påverka hela sjöns ekosystem. Lägre födokvalitet kan försämra djurplanktons och fiskars reproduktion, medan en ökad betydelse av heterotrofa processer kan förändra kolomsättningen och bidra till ökade växthusgasutsläpp vid islossningen. Sammanfattningsvis visar denna avhandling att vintern inte är en period i dvala, utan en central del av sjöars årliga cykel. Isens kvalitet och varaktighet, snötäcket samt tidpunkten och omfattningen av tillrinning är avgörande faktorer som styr näringsvävens struktur och funktion under isen. Att förstå dessa processer är avgörande för att kunna förutsäga hur sjöar kommer att reagera på ett förändrat klimat.

Popular Summary

Lakes are dynamic ecosystems that connect land and water, and their food webs depend on the movement of energy and nutrients among different organisms. The energy that sustains these food webs comes from two main sources which are resources produced within the lake itself, such as phytoplankton and macrophytes, and materials entering from surrounding terrestrial ecosystems. Phytoplankton, which are microscopic algae living in the water, are particularly important because they convert sunlight and nutrients into organic carbon through photosynthesis. This carbon forms the foundation for higher trophic levels such as zooplankton and fish. Two key factors drive the growth of phytoplankton are light and nutrients. Light provides the energy needed for photosynthesis, while nutrients such as phosphorus and nitrogen supply the building blocks for cellular growth. During winter in the Northern Hemisphere, many lakes are covered by ice and snow, which drastically reduce light and temperature. Because of these harsh conditions, ice-covered lakes were long assumed to be biologically dormant, with little or no growth of organisms until spring thaw. However, recent studies have challenged this view and shown that under-ice ecosystems can remain surprisingly active. The degree of biological activity under ice depends largely on how much light can penetrate the ice. When ice is clear and snow cover is thin or absent, sufficient light reaches the water column to support photosynthesis and phytoplankton growth. In contrast, when snow accumulates or when the ice becomes white and opaque due to trapped air bubbles, light transmission decreases, leading to lower phytoplankton growth. Thus, both the duration and quality of the ice cover play key roles in regulating productivity during winter. Nutrients entering lakes during the ice-covered period are another important driver of growth under ice. Runoff from surrounding land can deliver pulses of terrestrial organic matter and nutrients such as phosphorus and nitrogen. Traditionally, it was assumed that these nutrients remained in the water until spring, when increasing light conditions would allow phytoplankton to take advantage of them. However, it is now clear that organisms remain active under ice and can respond to changes in nutrient and light availability before the ice-off in spring. Despite this, previous studies have mainly focused on processes occurring after ice-off, while much less is known about what happens below the ice and how food webs function during winter. This thesis addresses that gap by examining interactions in under-ice food webs and investigating whether phytoplankton and their consumers are active, and if so, what drives their growth. To fill this knowledge gap, this thesis combined the usage of available data from previous studies and from the Erken monitoring program (paper I-II), an experimental setup in the lake Erken (paper III) and a field sampling campaign across six lakes (paper IV). In brief, this thesis shows that phytoplankton growth can depend on changes in light conditions following the composition of the ice cover, and the presence of snow on the ice. Specifically, thicker snow cover on ice, and increased thickness of white ice compared to clear ice, reduced phytoplankton growth under ice (paper I-II). In addition to the light conditions below ice, this thesis also showed that the duration of ice cover can be important for growth of phytoplankton after ice-off. Shorter ice periods were associated with lower phytoplankton growth after ice-off, likely because earlier melting led to increased mixing and turbidity, which limited light availability for photosynthesis. These findings highlight how changes in ice properties can alter the timing and magnitude of primary production in lakes. In addition to changes in light following ice cover, this thesis highlights the importance of nutrients and organic matter inputs in stimulating growth of organisms under ice. An experimental approach manipulating the timing of nutrient additions showed that phytoplankton growth under ice can increase with nutrient availability, if light is sufficient (paper III). When nutrients were added late in the winter season, closer to spring, phytoplankton increased in biomass. However, when nutrients became available earlier, growth was dominated by mixotrophic phytoplankton, species that can both photosynthesize and feed on organic matter or bacteria. This suggests that the composition of the plankton community under ice depends on the interaction between light and nutrient availability. Early nutrient input, when light levels are still low, favours organisms capable of heterotrophy, whereas later nutrient additions under brighter conditions support growth of broader phytoplankton community. A field study across six lakes (Paper IV) expanded the understanding of runoff-stimulated growth under ice by examining how terrestrial organic matter inputs influence under-ice food webs. Lakes receiving higher amounts of dissolved organic matter (DOM) from terrestrial ecosystems had stronger heterotrophic signatures in their food webs. High DOM likely stimulated bacterial growth, which increased the contribution of the microbial loop to energy transfer. However, these same conditions also lowered the nutritional quality of the food web because bacteria and terrestrial carbon lack essential polyunsaturated fatty acids (PUFAs). Phytoplankton, in contrast, produce these important biomolecules that zooplankton and fish rely on for growth and reproduction. Interestingly, the study also revealed spatial variation in resource use within lakes. In open-water (pelagic) habitats, zooplankton relied more on phytoplankton-derived carbon, while in shoreline (littoral) habitats, they depended more on bacteria and terrestrial material. This indicates that even during winter, under-ice food webs are not uniform but are likely structured by differences in terrestrial input, light and mixing, across habitats.

Together, these results show that under-ice ecosystems are far from inactive. Instead, they are shaped by a complex interaction between light and nutrients, related to ice properties and runoff regimes. The findings emphasize that the ice-covered period is an active and ecologically important season that can influence biological processes well beyond winter. Changes in the quality and duration of ice cover can shift the balance between autotrophic, mixotrophic, and heterotrophic pathways in lake food webs. Clear ice and high light penetration support high-quality autotrophic taxa such as diatoms, while low-light conditions under snow and white ice promote mixotrophs that can maintain productivity of lake ecosystems under ice, but produce food of lower nutritional value. These shifts in resource quality can cascade through the food web, ultimately influencing zooplankton growth, fish recruitment, and nutrient cycling. The implications of these findings are particularly relevant in the context of climate change. Winters are warming rapidly, and many northern lakes are experiencing shorter and less stable ice-cover periods, more frequent freeze–thaw cycles, and increased formation of white ice. At the same time, higher winter precipitation and rain-on-snow events are expected to increase runoff into lakes. These combined changes are likely to decrease light transmission under ice while delivering more nutrients early in the winter season. Such conditions could favour mixotrophic and heterotrophic production at the expense of high-quality autotrophic production, reducing the nutritional quality of resources for consumers. In the long term, such shifts in nutritional quality could have far-reaching consequences for lake ecosystems. Lower resource quality can limit zooplankton reproduction and fish recruitment success, while increased reliance on heterotrophic pathways could alter carbon cycling, potentially increasing greenhouse gas emissions when ice melts. Overall, this thesis demonstrates that winter is not an inactive period but a critical phase in the annual cycle of lake ecosystems. Ice quality and duration, snow cover, and the timing and magnitude of runoff are all key factors controlling the structure and function of under-ice food webs. Recognizing and understanding these winter processes is essential for predicting how northern lakes will respond to ongoing climate change.

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> *"Light thinks it travels faster than anything, but it is wrong. No matter how fast light travels, it finds the darkness has always got there first, and is waiting for it."* — Terry Pratchett

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