Combining limnology and paleolimnology:
A refined understanding of environmental sediment signal formation in a varved lake

Dominique Béatrice Maier
Better together.

To my family.
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Abstract

Paleoclimatic archives, such as lake sediments, extend our understanding of terrestrial and aquatic ecosystem dynamics in relation to climate variability beyond the period covered by instrumental data. In this context, annually laminated (i.e. varved) lake sediments are particularly valuable, as they offer high temporal resolution and undisturbed sediment. However, in order to extract reliable climate information from lake sediments, a careful calibration with the processes controlling the sediment formation is essential. This thesis combines limnological and paleolimnological data from a varved, boreal lake in northern Sweden (Nylandssjön, Nordingrå) collected over different time scales. The main aim of the thesis is to gain a more refined insight into which processes are reflected in the sedimentary diatom assemblage. More specifically, sequential sediment trap records were coupled with physical, chemical and biological lake monitoring and environmental data for comparison and validation with the varved sediment record. The main result of the thesis is that timing, succession and inter-annual variability of key limnological and environmental processes (e.g. ice-cover duration, lake over-turn or catchment run-off) are of major importance for the sedimentary diatom assemblage formation. Continuous monitoring of physico-chemical parameters over three consecutive years identified varying winter air temperature as a major factor influencing in-lake processes and hence the diatom record. Timing of lake over-turn and catchment run-off seemed to be the driver for monospecific diatom blooms, which are reflected in the annual sediment signal. The integrated annual diatom signal in the sediment was dominated by spring or autumn blooms, resulting either from a *Cyclotella glomerata* dominated spring bloom after relatively warm winter conditions, or a *Asterionella formosa* dominated autumn bloom after relatively cold winter conditions. The analysis of the diatom stratigraphy in the varved sediment over several decades corroborated the importance of climatic variables (late winter air temperature and NAO), even though the variables with the most predictive power for variance in the diatom data were associated with sediment composition (C, N and sedimentation rate) and pollution (Pb and Cu). Overall, the analysis of the drivers of inter-annual and decadal diatom assemblage fluctuations emphasizes the importance of winter air temperature, indicating that weather extremes may be disproportionately represented in annual sediment records in contrast to nutrient concentrations or sedimentation rate.

**Key words:** varved lake sediments, diatom sediment signal formation, sequential sediment trap, seasonal process timing, ice thinning, varve compaction, climate impact, catchment properties.
## Abbreviations

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tbody>
<tr>
<td>CCA</td>
<td>canonical constrained analysis</td>
</tr>
<tr>
<td>DCA</td>
<td>detrended correspondence analysis</td>
</tr>
<tr>
<td>DIN</td>
<td>dissolved inorganic nitrogen</td>
</tr>
<tr>
<td>DMAR</td>
<td>dry mass accumulation rate</td>
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<tr>
<td>DNA</td>
<td>deoxyribonucleic acid</td>
</tr>
<tr>
<td>DOC</td>
<td>dissolved organic carbon</td>
</tr>
<tr>
<td>NAO</td>
<td>North Atlantic Oscillation</td>
</tr>
<tr>
<td>NH4</td>
<td>ammonium</td>
</tr>
<tr>
<td>NO3</td>
<td>nitrate</td>
</tr>
<tr>
<td>NOAA</td>
<td>National Oceanic and Atmospheric Administration</td>
</tr>
<tr>
<td>OM</td>
<td>organic matter</td>
</tr>
<tr>
<td>PO4</td>
<td>phosphate</td>
</tr>
<tr>
<td>RDA</td>
<td>redundancy analysis</td>
</tr>
<tr>
<td>Si(OH4)</td>
<td>dissolved Silica</td>
</tr>
<tr>
<td>SMHI</td>
<td>Swedish Meteorological and Hydrological Institute</td>
</tr>
<tr>
<td>TN</td>
<td>total nitrogen</td>
</tr>
<tr>
<td>TOC</td>
<td>total organic carbon</td>
</tr>
<tr>
<td>TP</td>
<td>total phosphorous</td>
</tr>
<tr>
<td>TSM</td>
<td>total suspended matter</td>
</tr>
<tr>
<td>WD-XRF</td>
<td>wavelength dispersive X-ray fluorescence spectrometer</td>
</tr>
<tr>
<td>$Z_{\text{mix}}$</td>
<td>depth of mixed layer</td>
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List of papers

This thesis is based on the following four studies, referred to in the text by their Roman numerals:

Paper I


Paper II

Maier D. B., V. Gälman, I. Renberg, and C. Bigler. Using a decadal diatom sediment trap record to unravel seasonal processes important for the formation of the sedimentary diatom signal. Manuscript.

Paper III


Paper IV


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Author contribution

Paper I
DBM, CB and SD developed the scope of the paper. DBM and CB designed and conducted the fieldwork. DBM and CB conducted sample analysis. Data analysis and writing of the manuscript was conducted by DBM with input from all co-authors.

Paper II
DBM, CB and IR developed the scope of the paper. DBM, CB and IR designed and conducted the fieldwork. Sample analysis was conducted by DBM and VG. Data analysis and writing of the manuscript was conducted by DBM, with input from all co-authors.

Paper III
DBM, IR, NJA and CB conceived the study. Data collection was carried out by CB, NJA and JR. CB and DBM analyzed the data and wrote the manuscript, all authors contributed to the final version of the manuscript.

Paper IV
DBM, CB and IR developed the scope of the paper. DBM, CB, JR and IR conducted the fieldwork. Sample analysis was conducted by DBM, CB and JR. Data analysis and writing of the manuscript was conducted by DBM with input from all co-authors.

Authors
Introduction

Paleolimnology

Global climate change is expected to have wide-ranging effects on ecosystem functioning (Vitousek et al. 1997, 1994). Yet, the power of observational and experimental research to investigate long-term ecological dynamics beyond decadal timescales is limited. The analysis of paleoclimate archives such as lake sediments can complement the study of modern ecosystems, providing a pivotal tool to infer past environmental and ecological changes.

Paleo-archives can be of aquatic (marine or lacustrine sediments) or terrestrial origin (ice-cores, peat bogs, tree-rings). Lake sediments comprise biological and biogeochemical proxies, which can give indications of climate- and catchment-driven landscape development covering the Holocene and beyond (Meyer-Jacob et al. 2015). For the interpretation of shifts in chemical, atmospheric, catchment or aquatic properties biological lake sediment remains are a particularly reliable proxy (Bennion et al. 2010, Battarbee et al. 2012). The remains of aquatic organisms buried in lake sediments such as chitinized cladocera (water fleas), siliceous chrysophyte scales and cysts or diatom frustules (cell wall of benthic or pelagic micro-algae), or ancient DNA (Poinar and Cooper 2000, Graham et al. 2016) are valuable indicators of certain environmental conditions.

Key controls on diatom assemblages can include physical (temperature, light), chemical (pH, DOC, nutrients) and biological (grazing) factors (Battarbee et al. 2001). Common categorizations of diatoms (as, e.g., pH or phosphorus sensitive taxa) have allowed the interpretation of sediment assemblage shifts over time as they are directly related to nutrient pollution such as anthropogenic eutrophication (Bennion et al. 1996) or acidification (Renberg et al. 1993). Qualitative findings of historical nutrient pollution were made more quantitative through the use of transfer functions (Oksanen et al. 1988), a seminal method quantifying diatom-environment relationships based on space for time substitutions. However, while this method of calculating numerical values works for some chemical variables which directly control diatom assemblage shifts over time (Bennion et al. 2005), the application of transfer functions to reconstruct more complex acting climate drivers which impact diatom assemblages indirectly is not as reliable (Juggins et al. 2013).

Other paleolimnological methods to provide insight into climate related processes such as multiproxy approaches cannot be universally applied because
the behavior of physical and chemical control mechanisms varies between lakes and regions. An additional major difficulty for reliable biological proxy based inferences is the co-variation between eutrophication and temperature effects on ecosystems (Battarbee et al. 2012). Important study sites to avoid the confounding effects of human activity and better understand the role of underlying climatic controls are remote alpine or arctic lake sediments, where simultaneously the effect of warming is most pronounced (Smol et al. 2005; Battarbee et al. 2012).

Sediment signal transfer

To ultimately extract reliable information about physical, chemical or biological processes involved in the build-up of diatom stratigraphies, it is necessary to understand all steps involved in the formation of the sediment signal (Fig. 1). First, knowledge about the ecological and climatic controls on the growth of major taxa need to be collected or experimentally generated (Saros et al. 2012, Battarbee et al. 2012, Williamson et al. 2009). This may require the collection of detailed limnological data on physical, chemical, and biological parameters over multiple years. Next, the biological and physical processes controlling the transport of diatom remains to the sediment need to be understood. This can be best achieved through the use of sequential sediment traps, in combination with data on lake physical structure and underlying climatic conditions. Finally, the preservation of this signal in the sediment, and the calibration of the sediment record to long time-series of environmental drivers must be carried out. This requires highly resolved sediment records with decadal to annual resolution such as varved lake sediments, along with data on climatic and catchment processes over a corresponding period (Lotter and Anderson 2012). Fulfilling all of these steps requires the combination of traditional paleolimnological methods with detailed limnological studies conducted over multiple years. Because of the intensive amount of work and the wide variety of methodological approaches required, few studies have used this comprehensive approach, potentially resulting in the failure to recognize the role of key drivers of diatom sediment signal formation.

One major control on diatom sediment assemblages that has been largely overlooked in paleolimnological studies, and in limnological studies more broadly, is the role of seasonal processes, particularly during winter and early spring. A growing body of literature emphasises the importance of the winter season for lake ecosystems (Hampton et al. 2015, 2016), and several paleolimnological studies have indicated the importance of spring for diatom
Combined studies

Over the last decade, the reconstruction of temperature driven diatom assemblage shifts in lake sediments has been a major question within paleolimnology (Smol et al. 2005; Ruehland et al. 2008; Saros and Anderson 2015). To achieve reliable inferences, the wide range of indirect temperature effects on ecosystems needs to be disentangled before drawing conclusions about atmospheric changes from, e.g., biological sediment remains. Here, limnological studies build the basis for a broad process understanding and need to be paired with paleolimnological studies (Saros 2009, Saros 2012). Several previous studies have taken this approach. For example, whole lake manipulations combined with sediment traps confirmed small *Cyclotella* taxa as an indicator for different mixing depth patterns (Saros et al. 2016), and a combined study where lake thermal structure was inferred based on sedimentary diatom taxa in lakes along a DOC gradient (Brown et al. 2016). However, despite these and several other examples, studies using combined limnological and paleolimnological approaches remain relatively rare.

Approaches towards combined studies

Often observational studies only provide spot samples for verification of paleo-records. This approach is not able to resolve the importance of climatic variation at the seasonal scale for lake processes and sediment diatom records. To be able to incorporate ecological process understanding into paleolimnological records, two important steps are necessary: firstly, we need to identify the driver combination involved in processes of biological proxy formation and secondly, we need to understand how those processes are reflected in the remains of the lakes sediment. To achieve these goals, two important tools that can be applied in paleolimnology are sequential sediment traps and varved sediments.
Sediment traps

Sediment traps allow for continuous sampling of sedimenting material through the seasonal cycle. Sediment traps are important in understanding the sediment diatom record, because the delivery of diatom remains to the sediments does not always match the patterns of diatom abundance in the water column. For example, in Lake Baikal it has been found that diatom remains often dissolve in the water column before reaching the sediments, and are therefore not reflected in the sedimentary record (Ryves et al. 2003, Bradbury 1988). Frequently, sediment traps have been used to highlight the importance of extreme events on sedimentation processes (Simola 1977); however, sediment traps also have the potential to identify important temporal variation within a more normal range of limnological conditions. Sequential sediment traps are a powerful tool for understanding seasonal processes, because they allow the collection of continuous, temporally-resolved data particularly during periods which are difficult to sample such as ice break-up (Flower 1991, 2016).

Varved sediments

The analysis of lake sediments provides access to time periods outside the timescales covered by observational data. One of the most important prerequisites in paleolimnology is the establishment of accurate age determination of the sediment section of interest via macrofossils, tephra, radiometric $^{210}$Pb dating (last 100 years) or radiocarbon dating (age of $^{14}$C deposition for larger time scales). Only accurate sediment chronologies allow for a correct interpretation of sediment increments (Battarbee et al. 2012). In this context, annually laminated lake sediments are ideally suited for paleoclimate reconstructions because they offer inexpensive, highly accurate chronologies due to the underlying limnological processes giving rise to varve formation. Varved lake sediments are of high value because of their absolute chronology, which allows to circumvent sediment dating insecurities. The formation of strictly annual laminations under anoxic conditions also allows for the exclusion of sediment displacement effects (Zolitschka 2007).

A second advantage of incrementally dated archives is the high resolution of distinct annual layers that allow for the analysis of seasonal deposits reflecting events important in the sediment signal transfer process (Ojala et al. 2014). The formation of a sediment varve can be related to a distinct time period from the winter-spring transition of one year to the winter-spring transition of the following year. Therefore, subsampling varve years assures that the sediment being analysed contains an annually integrated signal with accumulations of
spring, summer, autumn, and winter material. This is particularly important for comparison to long-term monitoring data such as water quality data, sediment trap records, or historical climate records. The ability to establish an accurate chronology allows direct annual comparison of sediment characteristics to observed conditions, making it possible to establish connections between sediment and environmental characteristics, which can then be applied in other systems where the chronology is less clear.

Aims of the thesis

The primary goal of this thesis was to refine which climatic and limnological processes are reflected in a diatom sediment signal, focusing on the question, how seasonal processes are affecting the sediment signal transfer.

The specific research questions are listed below and refer to the individual chapters (Fig. 1):

- Which limnological and atmospherical processes are reflected in an annual diatom sediment record (Paper I)?

- Similarities and differences of seasonal sediment signal transfer. Can we make general statements about how seasonal processes are transferred into a diatom lake sediment record (Paper II)?

- Which processes control the diatom assemblage in lake sediments over time? Can we discriminate between catchment, climate and sediment controlled processes driving a diatom assemblage over time (Paper III)?

- What can we learn about lake sediment compaction processes from recent varved lake sediments (Paper IV)?
Figure 1. Illustration of environmental processes relevant for sediment signal transfer and formation, which have been addressed in this thesis.
Materials and Methods

Study site
History and catchment
Lake Nylandssjön (Nordingrå, 62°57’N, 18°17’E, 35 m above sea level) is located near the northeastern coast of Sweden and was formed ca. 4000 years ago as a consequence of shore level retrieval due to crustal uplift after the retreat of the Scandinavian ice sheet.

The lake catchment (0.95 km²) alternates between clay and silt deposits. The northern and northwestern shores of the lake are used as agricultural land. The rest of the catchment consists of forested hills with thinly covered bedrock and a maximum elevation of 130 m. a. s. l. Forest clearing has been reported for the period between 2002 and 2014.

Morphometry, bathymetry and limnology
Nylandssjön is a headwater lake (surface area of 0.28 km²) with one small outlet on the north shore. The lake has two basins with a maximum depth of 14.3 m in the south and 17.5 m in the north end of the lake, where sampling took place (Gälman et al. 2006, Maier et al. 2013).

Nylandssjön is a dimictic boreal soft water lake with a residence time of ca. 5 years. The lake is ice covered between November-December until April-May with 10-60 cm thick ice. Lake over-turn occurs between April and May in spring and between October and November in autumn. Over the stratified period during the summer months, an oxygen free zone that can even reach up to 7 m below surface develops in the hypolimnion (Gälman et al. 2009a). Average Secchi depth is 3 m and annual nutrient averages are typical for a mesotrophic lake (TP 18 µg L⁻¹, TN 500 µg L⁻¹, TOC 6.4 mg L⁻¹).

Varved sediment
The long ice cover duration (between 130-185 days) and the anoxic conditions in the hypolimnion during most of the year allow for the formation of annual varves, which show a distinct seasonality (Fig. 2). Each varve is separated by a black winter layer, which is composed of very fine organic material, settling under stagnant ice-covered conditions (Gälman et al. 2008; Maier et al. 2013). In spring, the black layer is overlain by a light green layer formed during the spring bloom and a brown organic layer later in the year (Renberg 1981). The sediment of Nylandssjön is very organic rich and permanent varve formation in this lake
started with the beginning of cultural eutrophication about 100 years ago (Renberg 1986).

![Figure 2](image)

**Figure 2.** Freeze core of the varved sediment of Nylandssjön from the year 2007. The surface has been plained. Each year is separated by a black winter layer.

**Field sampling**

For the scope of this thesis, different sampling periods at Nylandssjön have been included, as the lake has been studied over different time scales. Because of the high scientific value of this natural archive, a series of freeze cores was collected starting in the 1970’s. For an improved understanding of the processes controlling sediment formation, a sequential sediment trap was installed in 2002 and regular monitoring of physical properties was initiated. Additionally, a broad chemical and biological lake water monitoring study was conducted between the years 2012 and 2015.
Monitoring

Between March 2002 and May 2015, the lake was monitored bi-weekly over the entire annual cycle. At the monitoring site vertical temperature and oxygen profiles in 1 m depth intervals were measured. In winter, the lake was sampled from the ice and ice thickness and ice cover duration were surveyed. During the ice-free season, the lake was sampled from a boat in the deep basin. Between March 2012 and May 2015 water samples for chemical analysis were taken in addition to the vertical physical properties and plankton sampling. Water samples for chemical analysis (nutrients, chlorophyll, etc.) were taken at 1, 5, 7, 10 and 16 m depth, pH was measured using a hand-held probe.

Sequential sediment trap

The sequential sediment trap (Technicap PPS 4/3, Fig. 3) is deployed in the north basin at a depth of 14 m, held vertical in the water column with a weight on the lake bottom and three buoys 2 m below the lake surface connected with a steel wire. At the bottom of the trap funnel, a motor rotates 12 sample containers, which were exchanged three times per year, in February, May and September. The frequency for the rotation of the containers was programmed based on expected seasonal flux. During high seasonal flux in spring rotation frequency was highest (5 days in May) and decreases between May and September (9 days) until the lowest rotation frequency was programmed between September and February (20 days).

Figure 3. (a) Sediment trap prepared for exchange on a float (b) to be moored in the middle of Nylandssjön.
With this scheme, the entire annual sediment flux of 15 years with high seasonal resolution could be collected. Because of trap engine failure, the years 2006, 2009 and 2010 and some additional data points were lost.

**Varved sediment**

The varved sediment has been sampled regularly since 1979 in winter (late March) with a freeze corer (method described in Maier et al. 2013; Renberg 1986). The freeze core series established by the repeated coring approach was the basis for all papers, particularly for paper IV. The freeze corer is a hollow and wedge shaped aluminum case, which is filled with dry ice before being lowered from the ice cover to the bottom of the lake and into the sediment. After freezing is completed and a sediment crust is frozen around the wedge the core can be retrieved and stored frozen.

**Lab analyses**

**Water chemistry**

Water samples from five different depths were analyzed for total and dissolved inorganic nutrients and organic carbon (TP, TN, DIN, NO₃, NH₄, PO₄ and TOC and DOC with a flow analyzer) dissolved silica (Si (OH)₄) with a spectrophotometer). Further, water from each depth sampled was filtered for chlorophyll a concentration (spectrofluorometer) on GF/F filters (0.7 μm pore size).

**Diatoms**

The frozen varved sediment was cut with a scalpel in a -20°C walk-in freezer. Each varve is separated by the black winter layer as the last layer of one varve. The core is cut from the top of the black winter layer to the following top of the next black winter layer. The sediment material for each varve was freeze-dried and weighed before further analysis. The same procedure was applied for the sediment trap material.

Freeze-dried material for each trap sample and varve was sub-sampled, and digested in hydrogen peroxide (H₂O₂) to degrade the organic material and retain the diatom frustules. The diatoms were suspended in water and microspheres were added as external markers (Battarbee and Keen 1982) before they were mounted on slides for microscopic counting based on standard literature (Krammer and Lange-Bertalot 1985, 1986 and 1991).
The taxonomical harmonization among different analysts was performed by matching all taxa individually, excluding rare taxa. The diatom stratigraphy was zoned by optimal partitioning, using sum-of-squares criteria (Birks & Gordon 1985), and assessing the number of significant zones by comparison with the broken stick model (Bennett 1996).

**Sediment**

The freeze-dried sediment samples were weighed for bulk density and dry mass accumulation rate (DMAR) determination. Organic matter (total carbon and nitrogen content) was combusted and chromatographically analyzed with an elemental analyzer (Perkin-Elmer 2400 CHNS/O) and remaining major and trace elements with a Bruker S8 Tiger WD-XRF analyzer.

**Environmental data**

Environmental data (air temperature, precipitation, discharge) for the period between 1953 to 2014 were obtained from the Swedish Meteorological and Hydrological Institute (SMHI) measured at the closest weather station or based on gridded data for the period after 2002. NAO index values were retrieved from NOAA (National Oceanic and Atmospheric Administration, USA).

**Numerical analysis**

Statistical analyses of diatom data are all based on relative abundance (percentage) (Paper III). Geochemical data (Paper III) were log transformed to achieve normal distribution. In Paper III, temporal patterns in the sedimentary diatom assemblage were assessed by DCA, which served as the basis to select for taxa response models. Constrained ordination methods (linear (RDA) or unimodal (CCA)) were used to explain diatom composition together with the three explanatory variables (sediment properties, pollution and climate data) in the variance partitioning (ter Braak 1986). A mixed linear model was applied for the assessment of varve thickness decrease (Paper IV).
Results and discussion

Seasonality of diatom and sediment flux

The analysis of the entire annual sediment flux for three completely enumerated years of the sediment trap record revealed a strong seasonality for diatom sedimentation (2012 and 2014) but also an alternative scenario of a more annually integrated sediment record build-up (2013) in the same lake (Paper I). When a strong seasonal pattern was evident, the diatom flux was dominated by a monospecific spring flux of Cyclotella glomerata. Seasonality in diatom flux was also the main driver of interannual variability within the 10 year diatom sediment trap flux (Paper II). Over this extended time period a similar spring but also an autumn pattern occurred. Spring flux dominated annual diatom records were also characterized by high relative abundance of C. glomerata during this extended study period, whereas autumn flux dominated records were characterized by high abundance of A. formosa (Paper II).

Experimental studies provide key ecological information on taxa specific nutrient uptake and facilitate a better understanding of preferential seasonal growth in a community context (Malik and Saros 2016). For Cyclotella taxa the direct effect of temperature (apart from changed physical water conditions) is of less importance than light and nutrient availability (Saros et al. 2012, Saros and Anderson 2015). The interplay of seasonal driven nutrient availability may be of importance for C. glomerata dominated spring and A. formosa dominated autumn fluxes. Hence, the occurrence of the one or the other bloom is likely driven by a combination of physical process timing and catchment connectivity (see following chapters).

Water column driven seasonality of diatom and sediment flux

The detailed vertical monitoring of water chemistry, biological biomass build-up (measured as chlorophyll a), physical water column structure, and ice conditions on a bi-weekly basis revealed that there was no single process controlling variability in diatom growth and sedimentation, and that annual averages of environmental conditions were poor predictors of the sediment diatom signal. Instead, the timing and sequence of several key processes driven by winter air temperature explained the contrasts between years with different sediment signals (Paper I). A number of studies suggested process timing of high importance under elevated temperature conditions (Salonen et al. 2009, Benson et al. 2012, Hampton et al. 2016, Contosta et al. 2016). Within the three
consecutive and climatically different years of this study, the different sediment signal formation (seasonally driven vs. annually integrated) was connected to the timing of biomass accumulation before or after lake over-turn, particularly during the spring. Ice cover plays an important role for the different timing of water column over-turn vs. biomass build-up. During warm winters, the timing of diatom growth and sedimentation can be affected both by reduced ice cover duration, and by reduced ice thickness which can contribute to under ice phytoplankton blooms by increasing light availability (Horvat et al. 2017). *C. glomerata*, a particularly good competitor under increased light conditions (Saros and Anderson 2015), benefits from this process. As a result, over the 13-year study period, years with a major *C. glomerata* spring flux were associated with above average air temperature in March and April (Paper I and II). In addition to the spring-dominated pulses of *C. glomerata*, similar build-up of monospecific blooms immediately before or during lake over-turn also occurred in the autumn. The direct physical downward transport of the bloom with subsequent lake over-turn is reflected in the annual diatom sediment signal (Paper I and II).

**Catchment driven seasonality of diatom and sediment flux**

**Leaching of dissolved nutrients**

The highest dissolved inorganic nutrient concentrations were measured at 1 m depth under ice in 2012 and 2014, and there were also increasing nutrient concentrations in autumn associated with increased seasonal discharge (e.g., 2013) (Paper I and II). Above average winter discharge was clearly connected with warmer winter air temperatures (Paper II). The relevance for diatom sediment signal build-up is that the delivery of nutrients during warm winters occurs progressively while the stratified layer under ice is still intact (Fig. 1), so under-ice diatom communities can benefit from higher light and nutrient availability (2012 and 2014, see chapter above). The results of Paper I and II support previous work suggesting that different winter run-off timing (Cortés et al. 2017) may be important for biomass accumulation (Pernica et al. 2017). Paper I presents empirical evidence of the importance of increased winter air temperature for increased connectivity between catchment and biological sediment signal formation. In contrast, during years with cold late winter air temperature (2013), spring-flood waters only entered the lake after the break-up of the shallow, stratified, “light-saturated” under-ice water layer. As a result, catchment-derived nutrients became available for phytoplankton uptake in completely different limnological conditions, with consequences for the seasonal timing of phytoplankton bloom (Paper I). The different availability of nutrients
in these two scenarios may change the relative abundance of specific taxa but also the competitive balance between major diatom groups (Tilman and Kilham 1976, Saros and Anderson 2015), reflected by species abundances as well as the timing of diatom sedimentation.

**Transport of particulate material**

In the 10 year sediment record from Nylandsjön, different intensities of seasonal diatom and sediment flux were potentially connected with periods of forest clearing in the lake catchment (2000-2001). A reduced sediment and diatom flux was observed until forest clearing occurred again in the catchment (2008-2009 and 2011-2012) (Paper II).

Although meteorological conditions mediate the interaction between catchment inputs and lake processes, land management practices can have a strong influence on the materials being delivered from the catchment to the lake. In Sweden, forestry practices are an important land management consideration. Previous studies have found a connection between forest clearing and an increase of *A. formosa* for lake Kassjön (Anderson et al 1995). Different watersheds can show a different response to forest clearing, dependent on climate and geology in the catchment (Grant and Wolff 1991). Forest clearing in the catchment of Nylandssjön mainly occurred on hills in the catchment, directly connected with the southern and eastern shore of the lake. The relative abundance of *A. formosa* increased but was not dominating the assemblage after forest clearance, even after 2008 when forest clearance started again (Paper II). The effect of forest clearance might have been masked by the exceptionally warm late winter conditions in 2012 and 2014 which favoured abnormally high *C. glomerata* spring flux instead.

**Seasonality represented in the sediment**

The sediment analysis of the diatom stratigraphy since the 1930’s revealed no major change in the diatom assemblage but distinct shifts in relative abundances of diatom taxa (Paper III). Variance partitioning was used to quantify the explanatory power of environmental variables (climate, nutrients and sediment properties) on the diatom assemblage shifts. Climate (winter-spring temperature, NAO index), geochemical proxies (sedimentation rate, C and N) and variables associated with pollution (Pb, Cu and P) statistically explained significant amounts of variance in the diatom assemblage. The significance of climate variables (10.8%) confirms findings of the analysis of seasonal sediment flux based on the sediment trap data (Paper I and II). Precipitation did not
significantly impact the diatom assemblage in the sediment which also confirms observations during the monitoring period, where no pattern in precipitation anomalies could explain dynamics of major diatom taxa better than above average discharge (Paper II). Despite the significant results for climate predictors, climate had weaker predictive power than sediment parameters and nutrients (20.8%) and pollution variables (23.1%) for the long-term sediment diatom record. Timing, size and location of reported forest clearing patches can be relatively reliably connected with increased diatom and sediment trap flux in different years, but not directly with any specific taxa (Paper II). These increased sediment fluxes associated with forest clearing justify the high score of sediment parameters in the variance partitioning (Paper III).

The lack of a stronger correspondence between annual climate predictors and annual diatom records is consistent with the results from the more temporally-resolved studies (Papers I and II). In those papers, we did observe important climatic effects on, e.g., the magnitude of the spring *C. glomerata* flux in 2012 and 2014, but because these processes were very dependent on the timing of the temperature increases and associated lake processes, they could not be resolved with annual or seasonal temperature averages. In addition to seasonal effects, which are difficult to observe in long-term averages, the sediment diatom signal could also be influenced by extreme weather events such as, e.g., fall precipitation, which may contribute to *A. formosa* growth and sedimentation (Paper II). Such extreme weather events (warm late winter air temperature, extreme rain events) are not prominent in annual averages of weather variables, whereas they can have a major influence on sediment diatom records (e.g., major fluxes in spring can account for 70% of an annual flux). This statistical imbalance of driver representation may be the reason for climate being less explanatory than sediment properties.

**Calibration of varved lake sediment**

Based on a freeze core collection generated with a repeated coring approach since 1973, the compaction of specific varves in the sediment of Nylandssjön was measured over time. Compaction was highest within the first 5 years after deposition (60%), primarily due to a decreasing water content but also organic matter decomposition (Paper IV). The year-to-year variability of varve thickness is well preserved despite compaction and decomposition, which could explain the different behavior of decomposition compared to water loss (Paper IV). Also a number of studies on sediment element stability (Rydberg et al. 2008, Gälman 2009b, Klaminder et al. 2012), lithogenic compounds (Boës et al. 2011) and
organic compound diagenesis (Gälman et al. 2008, Tolu et al. 2015) were based on calibrations with the Nylandssjön varved sediment core series.

The validation of complete annual diatom sequential sediment trap records with the diatom sediment records of the annual varves in Nylandssjön proved a very good correspondence of relative abundance of major taxa and was the basis for seasonal signal formation studies in Paper I and II.
Conclusions

The study of limnological processes is essential for the reconstruction of environmental conditions based on diatom stratigraphies. For a reliable validation of a sediment record with environmental processes and to avoid erroneous conclusions, the highest possible time-resolution in the sediment and for the monitoring of limnological and environmental studies need to be applied. For a full and gapless discrimination between seasonal inputs, continuous monitoring with a sequential sediment trap is essential. The more detailed the associated physico-chemical lake monitoring, the better the identification of drivers and their reconstruction.

A continuous monitoring of full years is critical to discriminate between the importance of different seasons. The diatom sediment signal build-up can mainly be seasonally driven but can vary between a major spring or autumn bloom or only annually driven signal. In years with warmer late winter air temperature, a spring dominated sediment signal was built-up from a spring bloom occurring already under thinning ice-cover before lake over-turn.

To assess the full range of possible seasonal scenarios, only long-term monitoring in one and the same lake beyond decadal time scales will reveal the full range of seasonal influence on diatom sediment signal formation. The analysis of the annually resolved sediment stratigraphy since AD 1930 significantly confirmed the importance of late winter air temperature but also sediment properties, biogeochemical signals and pollution explanatory for variance in diatom assemblage shifts.

Studying the processes in the sediment is as important as understanding the proxies it carries. Within the first 5 years, the sediment compaction is greatest due to loss of water content (up to 60%) and organic compounds. This highlights the importance of varved sediment to accurately reconstruct environmental conditions.
Outlook

The seasonal dependence of taxa dominating the relative abundance in a sediment stratigraphy based on limnological processes inter-connected with catchment processes provides a deeper insight into diatom sediment signal transfer, but the development of a more general statistical relationship between temperature-driven extreme weather events that can be applied in other lake systems remains to be established. Diatom records do not accurately allow for reconstructions of, e.g., mean annual or summer temperatures. However, future research should focus on developing season-specific meteorological indices for comparison with diatom records, because these may be more appropriate for paleoclimate reconstructions based on diatom stratigraphies. The results presented in this thesis should be useful in this regard. By using the right metrics, sediment diatom abundances of *C. glomerata* and *A. formosa* could contain information regarding the inter-connection of limnological processes with catchment run-off timing.

The ambiguity in the sediment diatom signal could be better resolved by incorporating complementary information from other sediment proxies into the analysis. A first step could be the more detailed analysis of phytoplankton community in the water column, and of the seasonal succession of phytoplankton groups, in order to disentangle the influence of process timing on diatom growth. To enlarge the understanding of the influence of limnological and catchment processes on whole aquatic ecosystem shifts, a similar sampling design could be implemented to calibrate sedimentary DNA. The analysis of occurrence of high diatom flux with organic matter characterization can deliver a deeper insight into the importance of catchment connectivity for biological sediment signals. Oxygen isotopes in diatom sediment remains already serve as a reconstruction tool but could largely benefit from a seasonal calibration.

The importance of under-ice processes revealed in these studies supports a growing consensus in the literature that the ice-covered period is not a biologically dormant period in lakes, but instead can contribute to a major fraction of annual diatom sediment signal build-up. Moreover, the under-ice period is not characterized by a static state, but rather by highly dynamic hydrological and biogeochemical conditions. Until recently, processes during the ice-covered period received little attention in the limnology literature, and virtually no attention in the paleolimnology literature. While much work remains before reliable methods for estimating winter conditions can be developed from sediment diatom records or other proxies, this work provides a valuable step
towards achieving this goal. This is particularly important in the context of global climate change, which is expected to have a disproportionate impact on winter weather conditions such as snowpack depth, snowmelt timing, and ice-cover duration.
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References


Gälman V., J. Rydberg, A. Shchukarev, S. Sjöberg, A. Martínez-Cortizas, R. Bindler, and I. Renberg. 2009a. The role of iron and sulphur in the visual


Meyer-Jacob C., J. Tolu, C. Bigler, H. Yang, and R. Bindler. 2015. Early land use and centennial scale changes in lake-water organic carbon prior to


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