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Avhandling

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Abstract

Regime shifts in lake ecosystems can occur in response to both abrupt and continuous climate change, and the imprints they leave in palaeolimnological records allow us to investigate and better understand patterns and processes governing ecological changes on geological time scales. This thesis aims at investigating palaeolimnological records of regime shifts in lakes during the Holocene to explore how lake ecosystems responded to climate changes and anthropogenic activities and to identify thresholds or tipping points that produced regime shifts. The thesis includes case studies of two Swedish lakes and a synthesis of recently published palaeolimnological records displaying regime shifts. In the first case study a detailed diatom record from Lake Kälksjön, west-central Sweden, was investigated for periods of abrupt ecological change associated with the 8.2 ka cooling event. Using change-point analysis we found two regime shifts in the diatom record: one in response to an abrupt erosion event at c. 8040 cal. yr BP, and another caused by climate warming following the 8.2 ka event. The study demonstrates that not only can regime shifts be detected in sediment records, they can also be quantified and statistically tested for, provided that the sampling resolution is high and the chronological control sufficiently precise. The second case study is focused on recent regime shifts between clear-water and turbid states in Lake Krankesjön in southern Sweden. We combined palaeolimnological records and limnological monitoring data, concentrating on the documented collapse of the clear-water state in 1975 and the subsequent recovery in the late 1980s, in order to increase our understanding of changing ecological patterns and processes in shallow lakes. We found that the shift from clear to turbid conditions was abrupt, while the recovery of the clear-water state was more gradual, and the complex and non-linear reactions of the lake to shifting conditions emphasizes the importance of careful lake and catchment management if a stabilization of the clear-water state is desired. In addition to these studies, the theoretical concept of regime shifts is expanded upon in our synthesis of palaeolimnological records with regime shifts, where we characterize the shifts as either smooth, threshold-like or bistable. The examples are also placed within a conceptual model of potential physical processes that produce regime shifts in lakes and the main drivers behind the shifts are identified: direct climate influence on lakes, climate influence mediated through the catchment, lake ontogenetic processes and/or anthropogenic forcing. This framework helps to elucidate the relationship between driver and regime shift dynamics and the type of imprint that the associated regime shifts leave in sediment records.

When detected, past regime shifts and palaeolimnological records offer rich opportunities to increase the understanding of ecosystem responses to climate changes and to evaluate the mean state and natural variability of lake ecosystems on timescales of decades to millennia. Palaeolimnological archives provide a perspective on whether the pre-disturbance ”natural” state that may be the target of restoration efforts is actually natural, or if it is an anomaly in lake history, and if this target is at all possible to reach or if it, due to shifting baselines and lake ontogeny, is no longer a realistic restoration endpoint. Furthermore, I argue that linking the timescales of contemporary ecology with palaeoecology/limnology may provide long-term records of lake history and opportunities to further disentangle the role of different forcings on lake ecosystems. An improved understanding of lake ecosystem dynamics and regime shifts in lakes through the cooperation of limnologist/ecologists and palaeolimnologists may better prepare us to face future climate change and to fully understand and perhaps mitigate the effects of global climate change on lake ecosystems.

Key words: palaeolimnology, regime shifts, thresholds, alternative stable states, climate change, ecosystem dynamics, diatoms, hydrocarbons, monitoring, lake sediments, shallow lakes, 8.2 ka event

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This thesis is based on three papers listed below, which have been appended to the thesis. Paper I has been published in the journal indicated. Paper II and Paper III have been submitted to the indicated journal for consideration.

Paper I: Randsalu-Wendrup L, Conley DJ, Carstensen J, Snowball I, Jessen C, Fritz SC (2012) Ecological regime shifts in Lake Kälksjön, Sweden, in response to abrupt climate change around the 8.2 ka cooling event. *Ecosystems* 15: 1336-1350.

Paper II: Randsalu-Wendrup L, Conley DJ, Carstensen J, Hammarlund D, Hansson L-A, Brönmark C, Fritz SC, Choudhary P, Routh J, submitted. Combining limnology and paleolimnology to investigate recent regime shifts in a shallow, eutrophic lake. Submitted to *Journal of Paleolimnology.*

Paper III: Randsalu-Wendrup L, Conley DJ, Carstensen J, Fritz SC, submitted. Paleolimnological records of regime shifts in lakes in response to climate change and anthropogenic activities. Submitted to *Journal of Paleolimnology.*

For Aet
who encouraged me to be a scientist

Contents

1. Introduction

Ecosystems often show a smooth response in relation to gradually changing conditions, shifting over long periods of time from one state to another. Throughout the Holocene, however, abrupt ecological change was a common phenomenon, often driven by abrupt climate change. Much of the research on abrupt shifts in the geological literature has had a palaeoclimatic emphasis and has assumed that abrupt ecological change is evidence of abrupt climate change (Williams et al. 2011). Yet not all abrupt ecological changes stem from abrupt climate change. Abrupt ecosystem change can occur in response to a small and/or continuous change in forcing (climatic or otherwise), and theoretical mathematical models underpinning this concept have been around for almost 40 years (Holling 1973; Noy-Meir 1975; May 1977). The terminology is varied (tipping points, regime shifts, critical transitions, ecological surprises, bifurcations etc.), but the underlying theory suggests that ecosystems are complex and governed by a mixture of external drivers, positive and negative feedback loops, and fast and slow processes. As a result, they can be resilient when subjected to an external forcing, such as climate change or enhanced nutrient loading, until an internal threshold is passed, resulting in a large and abrupt shift in ecosystem state (Scheffer et al. 2001; Scheffer and Carpenter 2003; Folke et al. 2004; Andersen et al. 2009; Williams et al. 2011).

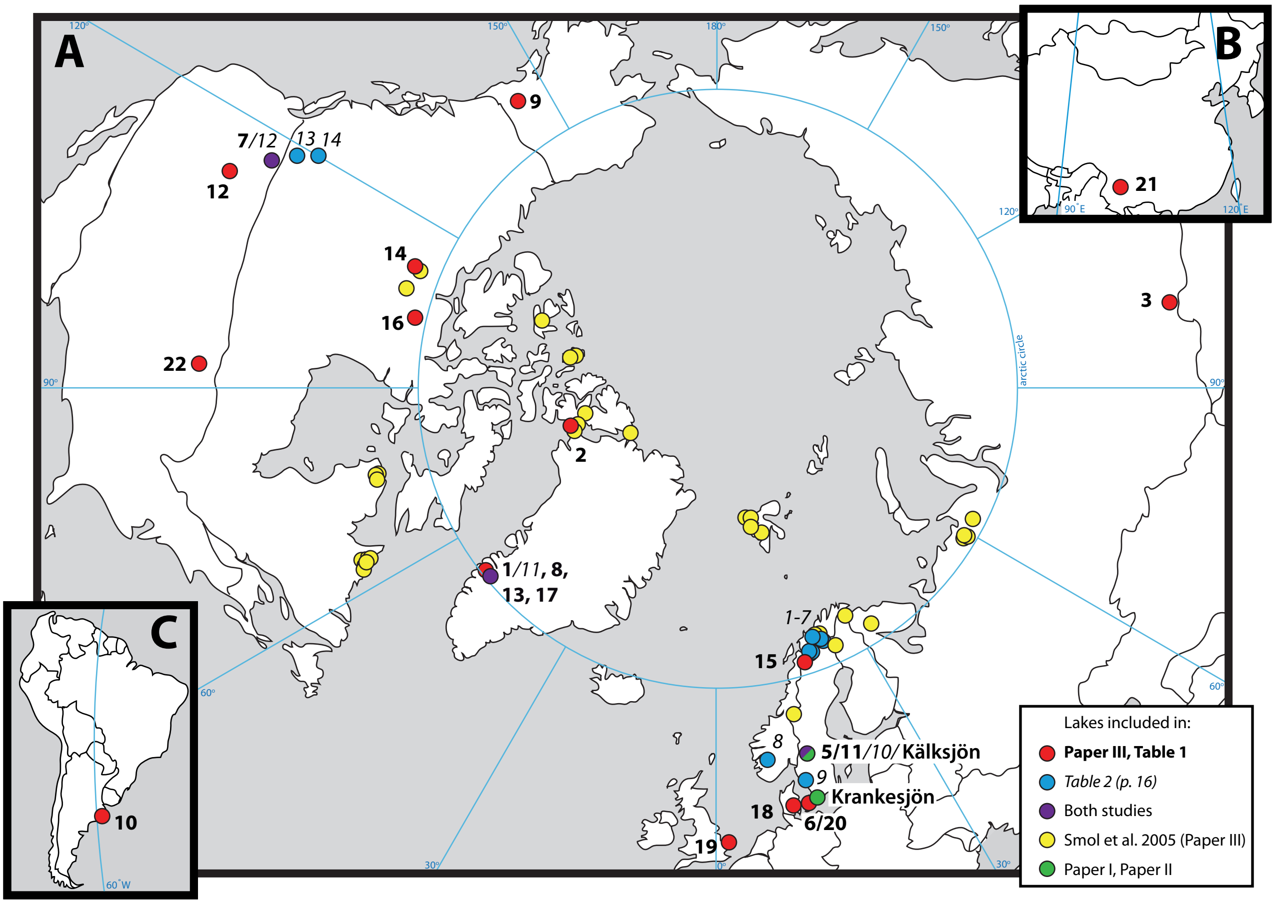

Figure 1. Map of (A) Northern Hemisphere, (B) China, (C) South America, showing the placement of lakes mentioned in the thesis. Red circles/bold numerals = lakes included in Paper III (Paper III, Table 1). Blue circles/italic numerals = lakes included in the investigation of the 8.2-event (Table 2). Purple circles = lakes included in both investigations. Yellow circles = lakes investigated by Smol et al. (2005), referenced in Paper III. Green circles = Lakes Kälksjön and Krankesjön, included in Paper I and Paper II. Lakes investigated by Rühland et al. (2008) and referenced in Paper III are not included in the figure.

Regime shift theory has been increasingly applied to various ecosystems, as well as in other systems, such as the human immune system, global climate and the world economy (Strange 2007). Recently, much of the ecological research has focused on developing statistical methods for detecting and quantifying regime shifts (Andersen et al. 2009; Carstensen and Weydmann 2012), as well as detecting early warning signals that might aid in the development of climate-adaptation strategies (e.g. Wang et al. 2012, but see Carstensen et al. 2013; Scheffer et al. 2012; Lindegren et al. 2012; Brock and Carpenter 2012). There is also increasing interest in using geological records to understand the patterns and processes governing abrupt ecological change on long time scales (Williams et al. 2011).

This thesis aims at investigating palaeolimnological records of regime shifts in lakes during the Holocene to explore how lake ecosystems responded to climate changes and anthropogenic activities and to identify thresholds or tipping points that produced regime shifts. This was accomplished through a synthesis of recently published palaeolimnological records displaying regime shifts, and two case studies: one of a lake ecosystem responding to abrupt climate cooling and subsequent warming 8200 years ago, and one of a lake displaying recent regime shifts between clear-water and turbid lake states (Fig. 1).

When detected, past regime shifts offer rich opportunities to study the patterns and drivers of abrupt ecological change in response to climate change and lend important information on the mean state and natural variability of lake ecosystems on time scales of decades to millennia, with associated implications important for lake management and restoration efforts. Palaeolimnological records of past regime shifts can also serve as a testing ground for critical-threshold detection tools. The knowledge collected from palaeolimnological records, such as those presented in this thesis, is important for fully understanding and adapting to the effects of future global climate change on lake ecosystems.

2. Summary of papers

2.1 Paper I

Randsalu-Wendrup L, Conley DJ, Carstensen J, Snowball I, Jessen C, Fritz SC (2012) Ecological regime shifts in Lake Kälksjön, Sweden, in response to abrupt climate change around the 8.2 ka cooling event. Ecosystems 15: 1336-1350.

In Paper I we investigated a detailed diatom record from Lake Kälksjön in west-central Sweden for periods of abrupt ecological change associated with the 8.2 ka cooling event. We analysed the diatom data for change points over time and found two sudden regime shifts. The first one occurred at *c.* 8040 cal. yr BP when an erosion event in the catchment led to an abrupt increase in nutrient supply to the lake, which resulted in a doubling of diatom biomass over 5-10 years. During the second event, at *c.* 7850 cal. yr BP, a large shift within the planktonic diatom community from taxa indicative of colder conditions to those indicating warm took place over 5-10 years. This shift occurred simultaneously with a successive change from periphytic to planktonic diatom dominance and a gradual diversification of the periphytic community, and the likely cause for the shift was climate warming following the 8.2 ka event. The cooling event itself did not have an equally large impact on the diatom community and was mainly registered as an increase in planktonic diatom *Puncticulata radiosa.*

2.2 Paper II

Randsalu-Wendrup L, Conley DJ, Carstensen J, Hammarlund D, Hansson L-A, Brönmark C, Fritz SC, Choudhary P, Routh J, submitted. Combining limnology and paleolimnology to investigate recent regime shifts in a shallow eutrophic lake. Submitted to Journal of Paleolimnology

Paper II is focused on recent regime shifts between clear-water and turbid states in Lake Krankesjön in southern Sweden. We combined palaeolimnological records and limnological monitoring data, concentrating on the documented collapse of the clear-water state in 1975 and the subsequent recovery in the late 1980s, to try to increase our understanding of changing ecological patterns and processes in shallow lakes. The shift from clear to turbid conditions was abrupt, occurring over one to two years, while the recovery of the clear-water state was more gradual. We also found that the system changed to a different clear-water state compared with that prior to the collapse, and the diatom community underwent a significant shift in 1978 when it changed to a less diverse, albeit ecologically similar, community. Despite rising phosphorus concentrations and lower abundance of submerged macrophytes, Krankesjön has remained in the clear-water state over the past 20 years, although this state seems to be increasingly unstable and susceptible to collapse.

2.3 Paper III

Randsalu-Wendrup L, Conley DJ, Carstensen J, Fritz SC, submitted. Paleolimnological records of regime shifts in lakes in response to climate change and anthropogenic activities. Submitted to Journal of Paleolimnology.

Paper III is a review in which we synthesised recently published palaeolimnological records displaying apparent regime shifts and characterized the shifts as either smooth, threshold-like or bistable. The examples were also placed in a schematic of physical processes that produce regime shifts in lakes to identify the main drivers behind the shifts:

Table 1. Author contributions to papers I-III

	Paper I	**Paper II**	**Paper III**
Fieldwork	I Snowball	L Randsalu-Wendrup D Hammarlund	-
Sample preparation	L Randsalu-Wendrup I Snowball	L Randsalu-Wendrup	-
Age-depth model	I Snowball	L Randsalu-Wendrup DJ Conley	-
Diatom analysis	L Randsalu-Wendrup	L Randsalu-Wendrup	-
Geochemical analysis	L Randsalu-Wendrup	P Choudhary L Randsalu-Wendrup	-
Pollen analysis	C Jessen	-	-
Collection and assembly of monitoring data	-	L-A Hansson C Brönmark L Randsalu-Wendrup	-
Numerical analysis	J Carstensen L Randsalu-Wendrup	J Carstensen L Randsalu-Wendrup	-
Literature review	-	-	L Randsalu-Wendrup
Data interpretation	L Randsalu-Wendrup J Carstensen DJ Conley SC Fritz I Snowball	L Randsalu-Wendrup C Brönmark J Carstensen DJ Conley SC Fritz D Hammarlund L-A Hansson J Routh	L Randsalu-Wendrup J Carstensen DJ Conley SC Fritz

direct climate influence on lakes, climate influence mediated through the catchment, lake ontogenetic processes and/or anthropogenic forcing. This framework serves to clarify the relationship between driver and regime shift dynamics and also sheds light on the imprint of regime shifts in sediment records, which can further our understanding of patterns and processes governing ecological changes on geological timescales.

3. Regime shift theory

The terminology and theory associated with regime shifts is diverse, and there is still no clear consensus on definitions and terminology. In Paper III we define the terms as follows:

A **regime shift** is a major ecosystem reconfiguration (in system structure, function and feedbacks) that is abrupt (occurring at rates that are rapid relative to background rates of change) and persistent (Folke et al. 2004; Lees et al. 2006; Andersen et al. 2009; Williams et al. 2011). It typically occurs at several trophic levels, affecting many of the ecosystem's state variables (Andersen et al. 2009; Crépin et al. 2012).

A **threshold/tipping point** is the point at which this abrupt change occurs, the place (in time) where a small change in driver can produce large responses in the ecosystem, and where a different set of system feedbacks become dominant (Dodds et al. 2010, Crépin et al. 2012). The existence of thresholds is key for demonstrating bistability or hysteresis according to Andersen et al. (2009), but the existence of a threshold does not always entail a regime shift; the state crossed into might not be persistent (Dodds et al. 2010).

We characterize regime shifts according to three scenarios as described by Andersen et al. (2009) (Fig. 2):

Type I: ”smooth” pressure-status relationships, where an abrupt shift in the driver (e.g. climate change or nutrient input) leads to an equally abrupt ecosystem change. Although nonlinearities may be present in the ecological system response, strong and rapid forcing (climatic or otherwise) is the primary causative agent of the abrupt ecological change (Williams et al. 2011). Because of the often inherently slow forcing of climate in comparison to the life cycles of organisms in limnological

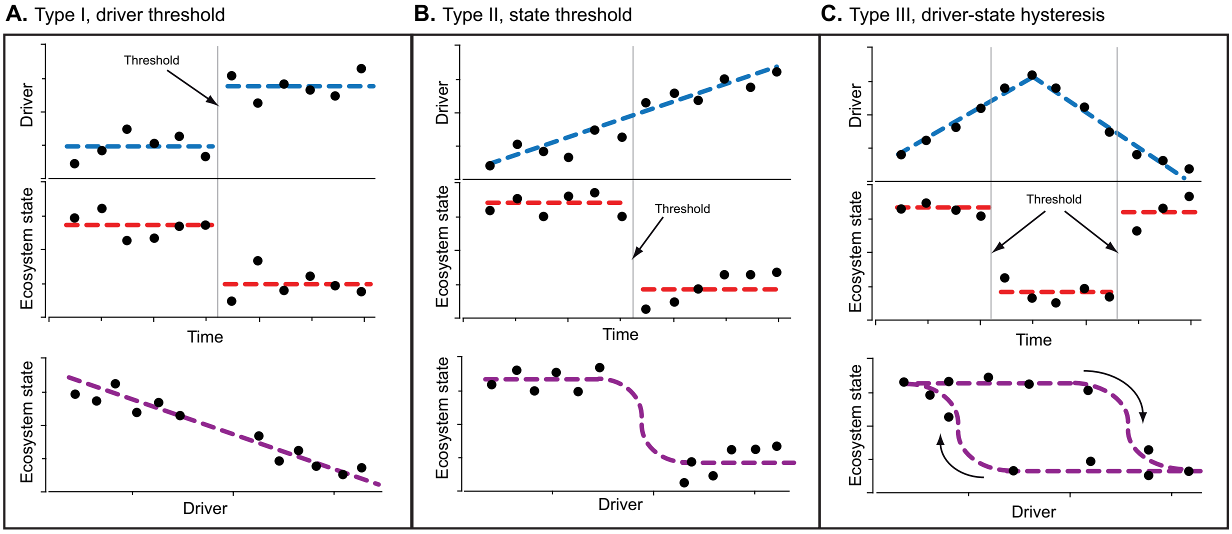

Figure 2. Three types of regime shifts. The two top rows show time series of driver (e.g. nutrient input) and ecosystem state (e.g. macrophyte cover), and the lower row shows the relationship between driver and ecosystem state. Grey vertical lines represent regime shifts. (a) Type I: smooth pressure-status relationships: the regime shift in the driver is linearly mediated to the ecosystem state. (b) Type II: threshold-like state responses: regime shift in ecosystem occurs after driver exceeds a threshold. (c) Type III: bistable systems with hysteresis: when the driver is slowly increased and then decreased again, the ecosystem jumps between two alternative states due to the hysteresis loop linking state and forcing; different ecosystem states can exist under the same conditions; in order for the system to change back to the "original" state the driver must exceed a second critical threshold, lower than the first. Redrawn from Andersen et al. (2009).

ecosystems, examples of smooth regime shifts are not very abundant in the palaeolimnological literature. The threshold is present in the forcing variable, and while clear examples of regime shifts and threshold dynamics within the climate system derived from palaeoclimatic data exist (e.g. McNeall et al. 2011; Shuman 2012), relatively few studies have examined how the crossing of these climatic thresholds affects ecosystems.

Type II: threshold-like state responses, or tipping-point regime shifts, where the change in driver does not affect the ecosystem response variable until a critical ecosystem threshold is reached, at which point the system state changes rapidly (Andersen et al. 2009). The forcing is progressive and gradual, although often overlaid by higher-frequency variability, and abrupt ecological change is driven by internal dynamics in the ecological systems. Since the internal dynamics are strongly governed by site-specific factors, such as catchment characteristics, lake depth, biological competition, and disturbance, local responses to a common regional forcing may be heterogeneous (Williams et al. 2011). In Paper III, we find that many examples of climate-related regime shifts in palaeolimnological records fall into this category.

Type III: bistable systems, which exhibit hysteresis behaviour with two alternative regimes during increasing and decreasing modes of the driver (Box 1, p. 8). A single transition from one state to another is the same for the non-linear threshold and the hysteresis responses, and evidence for hysteresis can only be shown with data where the forcing variable is in decline following a regime shift (Collie et al. 2004; Wang et al. 2012). Thus, it may be difficult to demonstrate that a discontinuous regime shift has taken place: in modern environments stresses are often continuously increasing (Wang

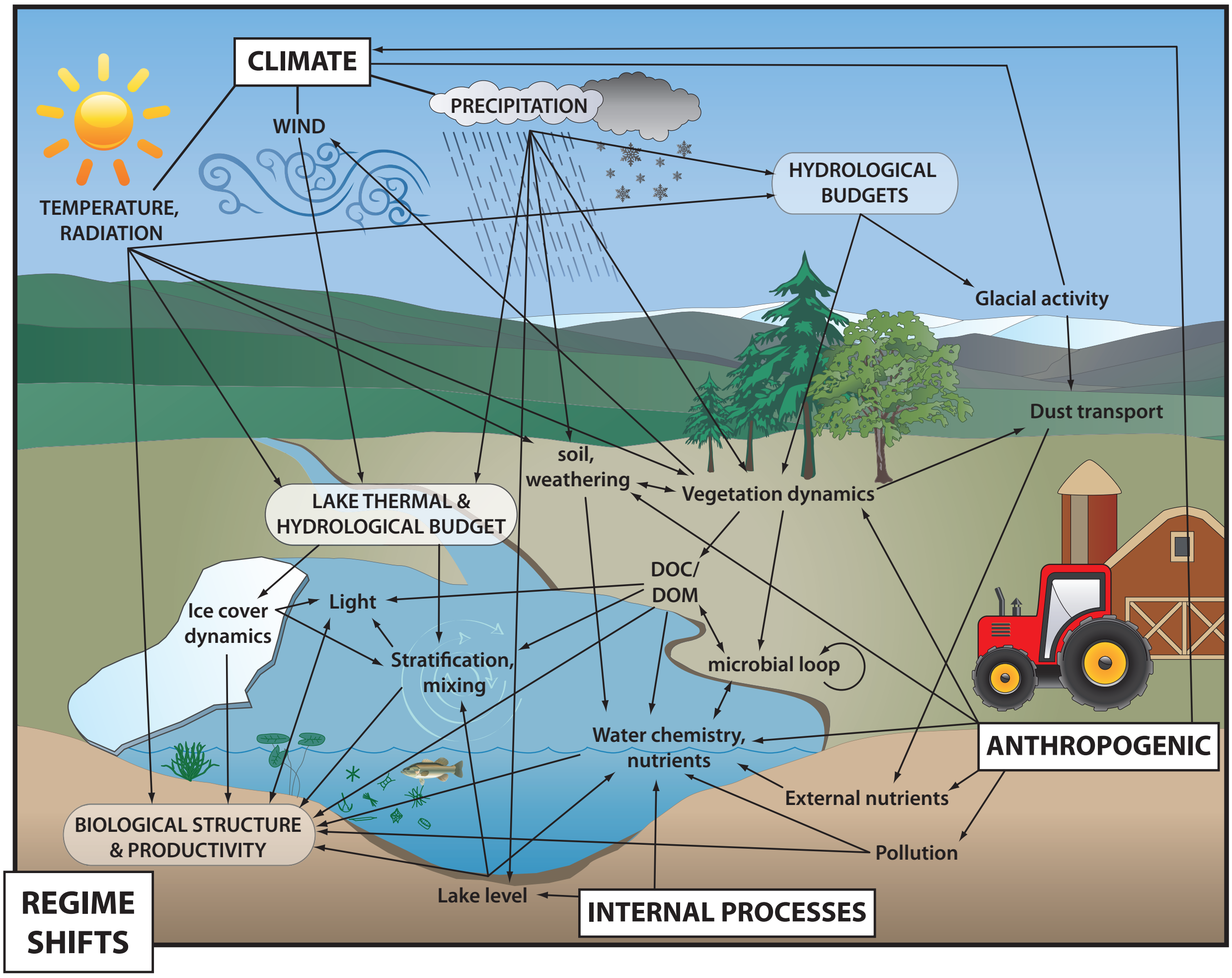

Figure 3. A conceptual model showing principal physical processes causing regime shifts in lakes. Modified from Fritz and Anderson (2013).

et al. 2012), and in palaeolimnological studies it is often difficult to evaluate whether different states exist under the same conditions due to the quality of records and because of processes associated with lake ontogeny and shifting baselines (Box 1). The smooth and threshold-like changes (Type I and II) are reversible along the same trajectory when the driver or forcing variable is reversed, whereas in a bistable system with hysteresis, the critical threshold for a shift from regime 1 to 2 differs from the critical threshold for a return shift from 2 to 1, because the different regimes have different sets of stabilizing feedbacks. As a consequence, regime shifts in bistable systems may be very difficult, or even impossible, to reverse (Crépin et al. 2012).

Because of their sensitivity to environmental changes, and their responsiveness to changes in the surrounding catchment and atmosphere, lakes are outstanding sentinels of environmental and climate change (Battarbee 2000; Williamson et al. 2009; Adrian et al. 2009; Leavitt et al. 2009). The structure and functioning of a lake ecosystem is determined by complex interactions among climate change, human impact, in-lake processes, lake ontogeny and catchment properties (geology, soils, vegetation), all of which vary in time and space and may have considerable influence on biological structure, as well as act as information filters altering the climate signal as it enters the lake (Schindler et al. 2001; Anderson et al. 2004; Leavitt et al. 2009; Fritz and Anderson 2013) (Fig. 3). The strength of the feedback mechanisms maintaining current lake ecosystem state (resilience) is also determined by multiple factors, such as biological community, sediment type, lake depth and morphometry. Therefore the threshold at which a regime shift occurs, as well as the degree of reversibility, will differ among different systems, in the same way that ecosystem responses to the same forcing will

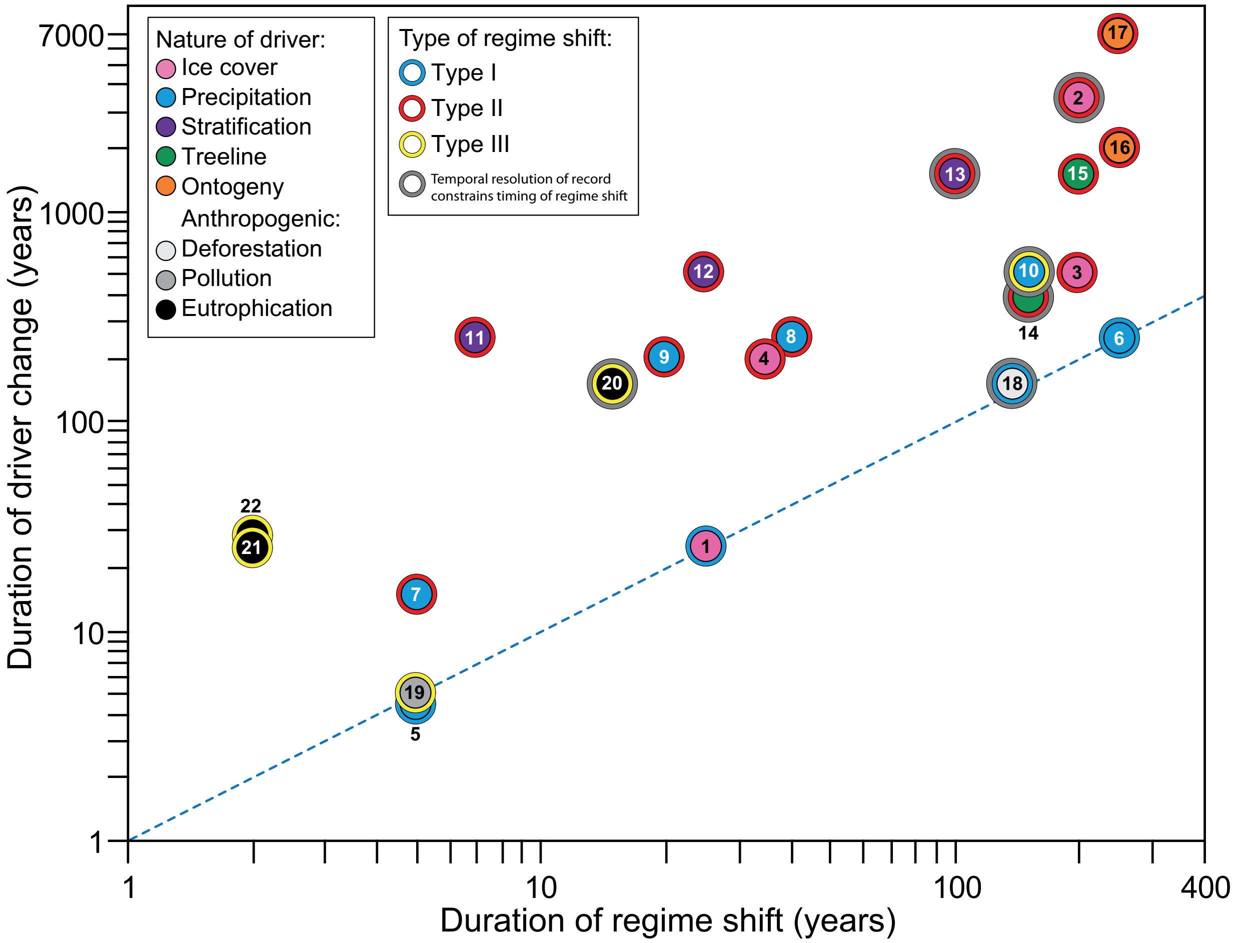

Figure 4. Duration of regime shift plotted against duration of driver change for studies investigated in Paper III. Numbers refer to reference numbers in Paper III, Table 1. Dashed blue line is a 1:1 line showing regime shift duration equalling duration of driver change.

differ and might also change over time within the same system: the same lake may display linear or hysteretic responses depending on local conditions (Crépin et al. 2012).

In Paper III we identify six main driver pathways leading to regime shifts in lakes:

1. climate - ice cover
2. climate - precipitation
3. climate - mixing and stratification
4. climate - catchment vegetation
5. lake ontogeny
6. anthropogenic forcing (including deforestation, pollution and eutrophication),

and we investigate the nature of lake responses according to the three types described in Andersen et al. (2009). Examining the relationship between the duration of change in drivers and the duration of the regime shifts (Fig. 4), we find that type I regime shifts fall on the 1:1 line, with forcing and response variables acting on similar timescales, while regime shifts of type II and III fall above the line, with regime shifts acting on a shorter time scale than changes in the drivers. This is in line with our conceptual model, but an important discrepancy highlights the significance of driver selection when classifying regime shifts: because the multitudes of drivers affecting lake ecosystems act on different time scales, the classification of an ecosystem response to a changing driver depends on which driver is the focus of the investigation. The discrepancy is Sayer et al.'s (2006) study of regime shifts in a shallow lake in response to the introduction of tributyl tin (TBT) as an antifouling paint on boats (Fig. 4, no. 19). They found that introduction of TBT in the 1960s caused regime shifts, with a dramatic loss of submerged vegetation, the replacement of macrophytes by phytoplankton and shifts in associated diverse animal communities (Sayer et al. 2006). We classify the shift as type III, but it displays type I-like behaviour with the shift from clear water to turbid conditions occurring as an immediate response to the change in driver (TBT). The ecosystem was influenced by slower drivers, such as eutrophication and increased salinity, which reduced the resilience of the system and made it more vulnerable to perturbations. The introduction of TBT became the proverbial straw breaking the camel's back and forced the system into a turbid state, which was then maintained even when TBT inputs were reduced. Thus, characterizing the transition as a type III regime shift is appropriate. With another focus, however, another classification might have been suitable.

A problem in working with palaeolimnological records in general, and when investigating regime shifts in particular, is low temporal resolution. In some of the literature in our synthesis, the regime shift occurs between two samples, but given a resolution of 150 (Bradshaw et al. 2005) or even 300-400 years (Rouillard et al. 2012) per sample, it is impossible to establish whether the shift has taken place over 100, 10 or even one year. However, in all of the examples the forcing is acting on even longer time scales (Fig. 4), allowing identification of the general dynamics behind the shifts although the specifics are hidden in the time integration inherent to sediment records. Resolution is also a confounding factor when discussing terminology and definitions: a shift in ecosystem state is generally considered a regime shift if it is abrupt and persistent (e.g. Andersen et al. 2009), but what is persistent on a geological time scale? Anderson et al. (2008), for example, describe a regime shift 8200 years ago where the system stayed in the new regime for 50 years before it shifted back again. In the perspective of modern day monitoring data, this period is long, and the regime persistent, but in some of the other studies presented in Paper III, the shift might not even be evident in the record due to low temporal resolution.

The strength of palaeolimnology in investigating regime shifts in lakes may not only be to look directly at individual changes, but to be able to use long sediment records to evaluate the mean state and variability of lake ecosystems on time scales of decades to millennia. This can improve contemporary studies where changes that we identify as regime shifts on one scale, might actually be part of the natural variability of the system: persistent for years or decades, but perhaps not longer. Understanding lake dynamics on long timescales is critical for lake management and restoration efforts: the palaeolimnological record provides a perspective on whether the pre-disturbance ”natural” state that may be the target of restoration is an anomaly or short-term state in lake history, and/wor whether, due to shifting baselines and lake ontogeny, this state is no longer possible to reach.

Box 1, hysteresis and shifting baselines

In the limnological literature, bistable systems with hysteresis are frequently described as having ”alternative stable states”, and the implications are often illustrated using ”landscapes” representing stability properties of the ecosystem state at different forcing conditions (e.g. Scheffer and Carpenter 2003; Figure 5). The ball represents the state of the ecosystem, and the size of the valleys illustrates the resilience of the system (i.e. the amount of perturbations the system can absorb without shifting to another state). If the system is on the upper branch and close to the threshold point (T_1), a slight increase in the driver may bring the system across the threshold and induce an abrupt change to the lower state or regime (forward shift). A backward shift occurs only if driver conditions are reversed far enough to reach the other threshold (T_2) and the difference between forward and backward shifts is known as hysteresis. A perturbation (arrow) may also induce a shift between states if it is sufficiently large to bring the system over the hilltops separating the valleys. Thus, gradual changes in the driver (for example climate warming) can act by reducing the resilience and increasing the fragility of the system, while leaving the ecosystem state apparently unaltered until a threshold is crossed (either with continuous change or through a perturbation), at which time an abrupt shift occurs.

Gradually changing external conditions may also inhibit the system from reverting back to the ”original” state upon changing conditions – while residing in the lower state, changes in forcing, such as CO_2 concentration, temperature, wind patterns, salinity or infilling of sediments (lake ontogeny), may preclude the system from returning to previous conditions (Duarte et al. 2009; Fig. 6). This process is often referred to as shifting baselines and may be of great importance for determination of lake restoration targets.

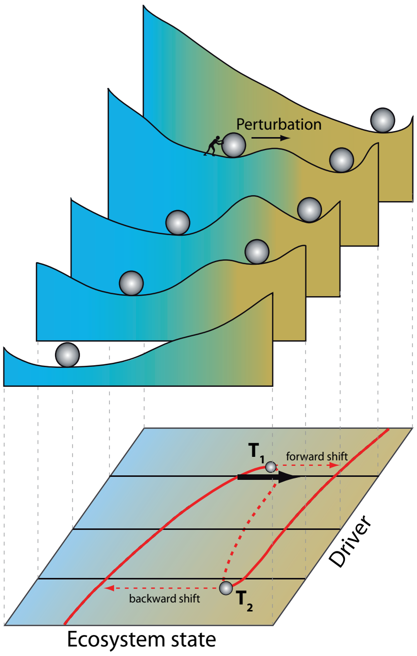

Figure 5. Stability landscapes illustrating how changes in the driver can affect the stability of the ecosystem state. Modified from Scheffer et al. (2001).

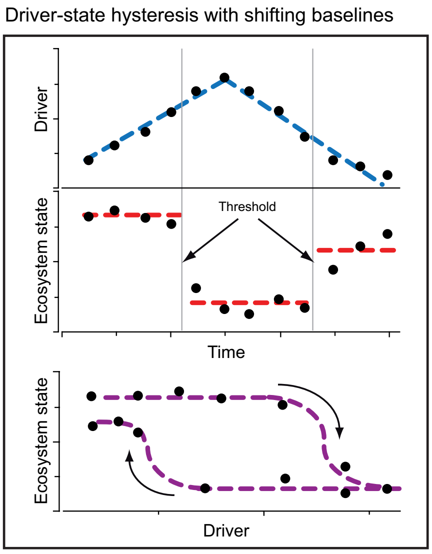

Figure 6. Driver-state hysteresis with shifting baselines. Changes in other forcing factors than the driver prevent the ecosystem from returning to the “original” state upon driver decrease. Inspired by Andersen et al. (2009) and Duarte et al. (2009).

4. Study areas

4.1 Kälksjön: site description, subsampling and chronology (Paper I)

Lake Kälksjön (60°90'N, 13°03'E) is located in the province of Värmland in west-central Sweden (Fig. 7). The lake has an area of 0.4 km^2, maximum water depth is 14.2 m, and it is located below the highest shoreline at an altitude of 98 m a.s.l. (Zillén et al. 2003). There are four inflows, entering from the east and north, and the lake drains through a stream to the west. The lake catchment covers 4 km^2 and is dominated by managed boreal forest (Zillén et al. 2003). Most of the catchment is covered by sandy and silty till, while areas close to the lake margin are dominated by silty and clayey soils, and some arable land occurs along the western shore of the lake (Zillén et al. 2003). Kälksjön became isolated from the sea at *c.* 9000 cal. yr BP and provides an ideal sedimentary environment for the study of abrupt ecosystem change, because the seasonal cycle of sedimentation is preserved in the lake in the form of biogenic-clastic varves (Zillén et al. 2003; Stanton et al. 2010; Snowball et al. 2010).

Four parallel sediment profiles were collected from the lake ice using a modified rod-operated Russian corer during fieldwork in the late winters of 2002 and 2003 (Snowball et al. 2010). The profiles cover a sediment thickness of 6.75 m each and include the entire post-isolation period (Snowball et al. 2010). Seventy-eight continuous and quantitative samples for analysis of diatoms, pollen and organic carbon content were taken using an aluminium tray of known volume. The sediments in the tray were cut to varves along the stratigraphic boundaries marking the division between winter and spring layers. The samples span the time period from *c.* 8500 to 7500 cal. yr BP, with a resolution of 20 varves between *c.* 8500-8300 cal. yr BP and *c.* 7700-7500 cal. yr BP and 10 varves in between. An initial varve chronology for the Kälksjön sediment sequence was established by Stanton et al. (2010), with an uncertainty at 8000 cal. yr BP on the order of 150 years. Snowball et al. (2010) reduced this uncertainty to 25 years through radiocarbon wiggle-matching of a 400-year-long section of Stanton et al.'s (2010) varve chronology that spanned the 8.2 ka cooling event. They also matched the GRIP and NorthGRIP ice-cores to the same absolute timescale by comparing ^{10}Be

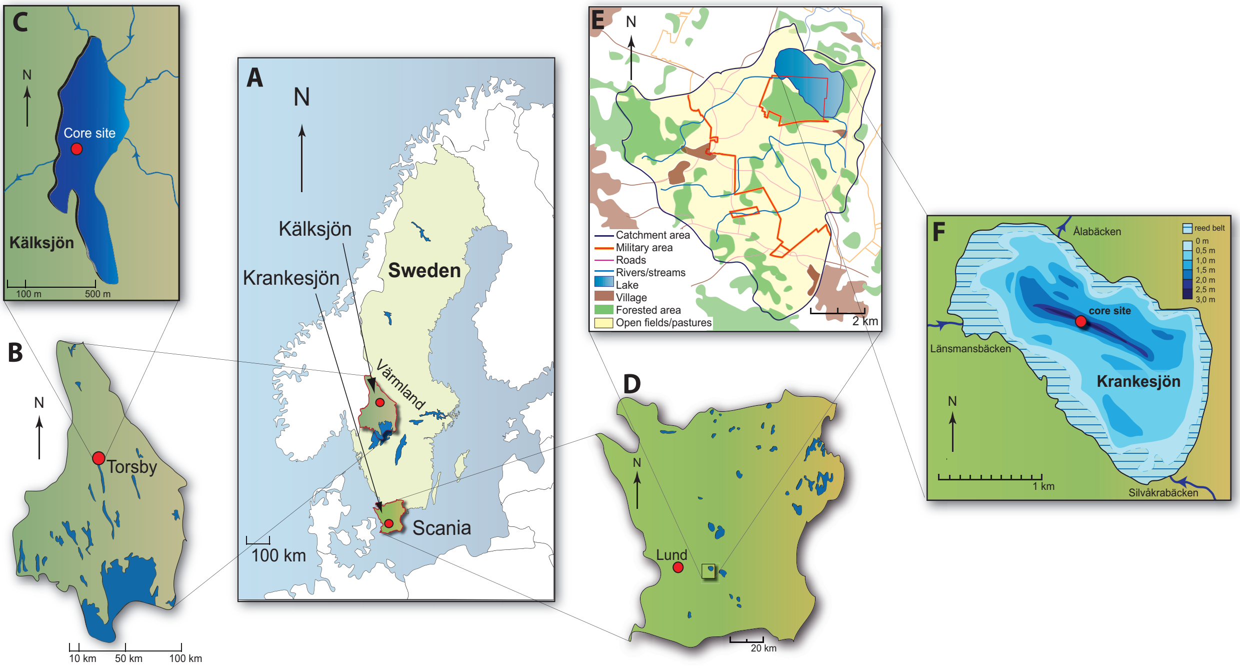

Figure 7. (a) Map of Scandinavia showing the location of Lake Kälksjön and Lake Krankesjön in Sweden (b) Map of the province of Värmland (c) Close-up map of Lake Kälksjön showing inlets, outlets and coring site (d) Map of the province of Scania (e) Map of the catchment area surrounding Lake Krankesjön (f) Close-up map of Lake Krankesjön showing inlets, outlet, bathymetry and sediment sampling site (partly redrawn from Stanton et al. 2010).

data and tree-ring δ^{14}C (Snowball et al. 2010). This procedure synchronized the Kälksjön record and the Greenland ice-core record to an absolute timescale, without any dependency on changes in proxy-climate parameters. Our chronology is based on the wiggle-matched varve chronology (Snowball et al. 2010), and all absolute ages referring to Kälksjön have an uncertainty of ±25 years.

4.2 Krankesjön: site description, subsampling and chronology (Paper II)

Lake Krankesjön (55°42'N, 13°28'E) is situated in the southernmost part of Sweden (Fig. 7). The lake is shallow (maximum depth 3.2 m, median depth 1.5 m), with a water retention time of 2.3 months, and it is moderately eutrophic and calcium-rich. It has an area of 3.4 km^2 with a 53 km^2 catchment dominated by permanent grassland (59%), open fields (17%) and forest (16%). The lake has two inflows: the small stream Länsmansbäcken, entering from the west, and another, Silvåkrabäcken, from the southeast. The stream Ålabäcken is the outlet in the northern part of the lake. The lake has a history of structural shifts between two alternative states: one clear and macrophyte-dominated and another turbid, algal-dominated, in spite of apparently very little change in external nutrient loading (Blindow et al. 2006; Fig. 8b). Krankesjön is considered a waterfowl habitat of international importance, and the clear water state of the lake is favoured from a conservation standpoint in managing the lake for waterfowl, as well as from a human perspective (better water quality, higher biodiversity and fewer problems with toxin-producing phytoplankton is associated with higher recreational values).

A 76-cm sediment sequence was collected from the lake ice in February 2009, using a crust-freeze sampler (Renberg 1981; Fig. 9a). The frozen sequence was subsampled at the Department of Ecology and Environmental Science at Umeå University into 151 contiguous samples, each 0.5 cm thick (except the uppermost sample covering 1 cm), using methods described by Renberg (1981) (Fig. 9b). The uppermost 14-cm part of the sediment sequence was analysed, providing 27 samples that were freeze-dried and homogenised prior to analysis of diatoms, biogenic silica and hydrocarbons. The samples were dated by ^{210}Pb, ^{226}Ra and ^{137}Cs by gamma spectrometry at the Gamma Dating Centre, Institute of Geography, University of Copenhagen, and ^{210}Pb ages were calculated using the constant rate of supply (CRS) model (Appleby 2001). The activity of unsupported ^{210}Pb in the sediment sequence is generally low (around 15 Bq m^{-2} y^{-1}), which could indicate temporary erosion at the site, and in combination with small sample sizes, the error bars on the radiometric data are rather large (Fig 8a). Application of the CRS dating model (Appleby 2001) to the unsupported ^{210}Pb data, constrained by ^{137}Cs, suggested a mean sedimentation rate of 0.15 cm yr^{-1} over the last approximately 100 years, with increasing rates from 0.4-0.7 cm yr^{-1} in the surface sediments (0-2 cm below water level). The resolution of the records is on average approximately 3 yr sample^{-1}.

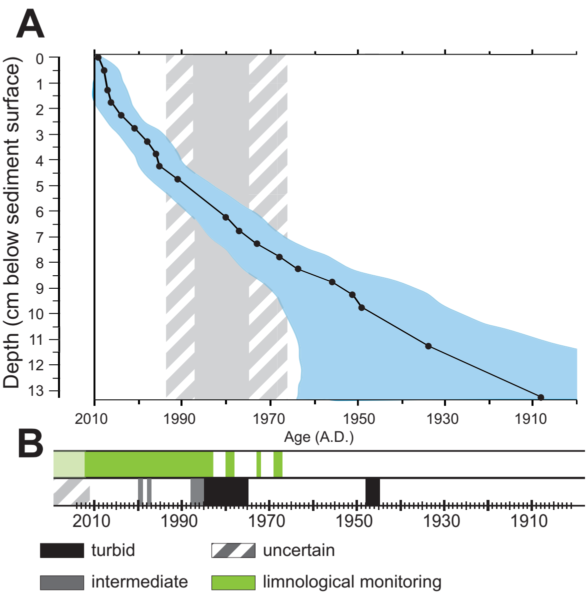

Figure 8. (a) Age-depth model for the Krankesjön sediment sequence based on ^{210}Pb-dating. The blue shading indicates dating uncertainty envelopes with 2σ error. Grey shading indicates turbid conditions with the dashed shading indicating dating uncertainty (b) Overview of the development of Krankesjön during the studied time period.

5. Methods

5.1 Diatom analysis

Diatoms (Bacillariophytae) are unicellular algae with siliceous shells (frustules) that occur globally in most types of aquatic environments. Most diatom species prefer a specific habitat and are either

Figure 9. (a) Sediment sampling in Krankesjön: Dan Hammarlund, Johannes Edvardsson and author (photo: Alice Nicolle), see also cover page to Paper II (b) Author subsampling in freezer in Umeå (photo: Petra Bragée)

planktonic (suspended in the water column) or benthic (associated with e.g. plants or stones, sand or mud in the littoral area). In addition to habitat preferences, diatoms are responsive to different physico-chemical conditions (temperature, light, turbulence, nutrients, pH, DOC, salinity etc.), and different species have developed sensitivity as well as tolerance ranges for different environmental parameters. Thus, past environmental conditions can be reconstructed through examination of diatom assemblages through time, and diatom analysis is a common method in paleolimnological and geological research. Their role as primary producers also makes diatoms excellent tools when searching for abrupt ecosystem changes in lakes.

Samples were collected from the sediments of Kälksjön and Krankesjön, freeze-dried and digested using the water-bath technique described by Renberg (1990a) with digestion using 30% H_2O_2 (Battarbee et al. 2001). Diatom concentrations (valves mg^{-1}) were determined by adding divinylbenzene (DVB) spheres to the cleaned samples (Battarbee and Kneen 1982). Cleaned subsamples were dried onto cover slips and mounted onto microscope slides using Zrax (R.I ~1.7+). At least 400 valves were counted in each subsample under a light microscope at ×1000 using phase-contrast optics. Diatom taxonomy followed Krammer and Lange-Bertalot (1986; 1988; 1991a; 1991b), Willams and Round (1987), Lange-Bertalot and Metzeltin (1996), Round and Bukhtiyarova (1996), Lange-Bertalot (1999), Håkansson (2002), Houk and Klee (2004) and Siver et al. (2005). Diatom results were expressed as relative abundances of each taxon, and as accumulation rates (valves cm^2 $year^{-1}$).

5.2 Pollen analysis

Samples for pollen analysis were prepared from Kälksjön sediments using standard methods and mounted on slides for further identification using a light microscope (Berglund and Ralska-Jasiewiczowa 1986). *Lycopodium* spore tablets were added for the calculation of pollen influx (Stockmarr 1971), and between 800 and 1000 pollen grains were counted per sample. Selected pollen data were shown as accumulation rates (grains cm^2 $year^{-1}$).

5.3 Organic carbon content

The total carbon content of the samples from Kälksjön was analysed using a Costech Instruments ECS 4010 elemental analyzer at the Department of Geology, Lund University. The subsamples were acid-washed in 10% HCl to remove trace amounts of carbonates, rinsed with deionized water and freeze dried prior to homogenization with a mortar and pestle. In Kälksjön the total inorganic carbon content is negligible (Snowball et al. 2010), and the total carbon content was assumed to equal the total organic carbon (TOC) content of the sediments and expressed as weight-% TOC.

5.4 Biogenic silica

Biogenic silica (BSi) analysis is a method that measures the amorphous silica content of sediments and is often used in lake sediments as a proxy for diatom abundance, and, in many systems, diatom productivity, as diatoms make up the most evident biological sink for Si (Conley and Schelske 2001; Struyf and Conley 2009). It is, however, difficult to separate the contribution of diatoms and other siliceous microfossils (chrysophyte cysts, sponge spicules, phytoliths) to the amorphous silica content (Conley and Schelske 2001, Finkelstein and Gajewski 2008), and microscopic analysis of siliceous remains is needed for determination of what sort of abundance the BSi record represents. If combined with diatom microfossil abundance data, it is possible to infer ecosystem-wide changes using biogenic silica data (Conley and Schelske 2001).

Biogenic silica concentration, expressed as weight-% SiO_2, was measured on sediments from Krankesjön using the wet chemical digestion techniques described by Conley and Schelske (2001).

5.5 Hydrocarbons

The hydrocarbon compositions of many algae and cyanobacteria are dominated by low molecular weight *n*-alkanes ($n\text{-}C_{15,17,19}$). In contrast, submerged and floating-leaved macrophytes have *n*-alkane distributions maximizing at C_{21}, C_{23} or C_{25} (Ficken et al. 2000; Meyers 2003). Hydrocarbons were extracted from the freeze-dried sediments of Krankesjön with a mixture of CH_2Cl_2 and MEOH (9:1 v/v). A Dionex Automated Solvent Extractor 300 was used (programmed for three extraction cycles at 1000 psi and 100°C). Extracted hydrocarbons were reduced in volume by using a Büchi Rotovapor and injected in pulsed splitless mode into an Agilent 6890 gas chromatograph equipped with a CIS-4 Gerstel inlet and DB5-MS column (30 m × 0.25 mm i.d. × 0.25 µm film); the oven temperature was held at 35°C for 6 min, increased to 300 °C at 5 °C min^{-1} and held there for 20 min. The chromatograph was interfaced with an Agilent 5973 mass spectrometer operated at 70 eV in full-scan mode (m/z 50– 500 amu). External and internal standards (S-4066 from CHIRON, Norway and deuterated perylene from Cambridge Laboratory, USA, respectively) were used for quantification. The results were expressed as ng per g dry sediment.

5.6 Monitoring data

Krankesjön has been the focus of many different research projects, as well as national and regional monitoring since the late 1960s, and we obtained and merged data sets from the Swedish University of Agriculture and the Aquatic Ecology Unit of the Department of Biology at Lund University and selected variables that aid in the understanding and description of the shifts between clear and turbid states that the lake has experienced. Water level data (year-round monthly measurements) from 1946 to the present (excluding 1990-1994) were obtained from the County Administrative Board of Skåne (Länsstyrelsen) and the Swedish Fortification Agency (Fortifikationsverket).

5.7 Numerical Analysis

Stratigraphic diatom assemblage zones (DAZ) were determined through regression tree analysis (De'ath and Fabricius 2000) of the diatom data using the mvpart package (De'ath 2012) for the R statistical software. The smallest tree within one standard error of the tree with the lowest cross-validation relative error was chosen. Detrended correspondence analysis (DCA) was performed using the vegan package (Oksanen et al. 2012) in R in order to establish the gradient lengths in the diatom data. In both Paper I and II the gradients were short (<2 SD units) and, therefore, principle component analysis (PCA) was performed on Hellinger transformed diatom data using the same package. Hellinger transformation preserved the Hellinger distances, a dissimilarity coefficient shown to exhibit good properties for ecological data, between samples in the resulting PCA (Legendre and Gallagher 2001). The number of significant axes was identified through comparison with the broken stick (null) distribution. One

PCA axis was identified as explaining significant proportions of the variance in the stratigraphic data when compared to the broken stick (null) model for both Kälksjön (expaining 47% of the variance) and Krankesjön (explaining 46% of the variance). For the Kälksjön data, principle components analysis was also performed on the planktonic and periphytic communities separately. In both the analyses one axis was significant, and these axes explained 61% of the variance in the planktonic community and 45% of the variance in the periphytic community, respectively.

5.7.1 Kälksjön specifics

Total diatom accumulation rates (DAR), the proportion of planktonic to total DAR, and the first principal components of both the planktonic and the periphytic communities were analysed for change points, i.e the points at which the statistical properties of a sequence of observations change, over time using a combination of abrupt step changes and piece-wise linear regressions (for details see Paper I; Carstensen and Weydmann 2012). Both models were equally good at describing the total DAR variations, but the step-change model used one parameter less and was considered more suitable for description of the trends in total DAR (Fig. 10). The model suggested that $\mathrm{DAR}_{\mathrm{total}}$ increased abruptly between 8041 and 8031 cal. yr BP. Changes were also apparent at the community level, and the first principal component of the plankton community was best described with a step-change model, suggesting abrupt changes around both 8201 and 7851 cal. yr BP (Fig 10).

5.7.2 Krankesjön specifics

Yearly means (March-September) of phosphorus, nitrogen, chlorophyll-*a*, turbidity, pH and Secchi depth were calculated from the monitoring data (all log-transformed except pH and Secchi depth) as marginal means from a General Linear Model that accounted for differences in months of sampling across years (Carstensen et al. 2006). Means of log-transformed variables were back-transformed using the exponential function to represent geometric means.

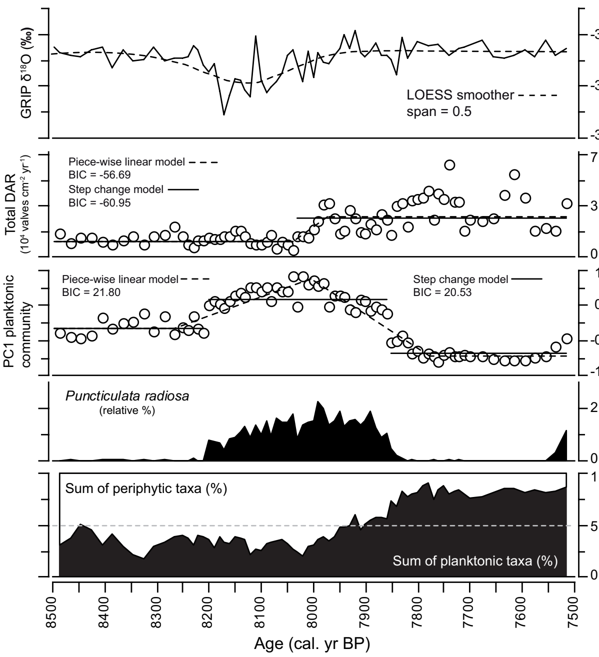

Figure 10. $\delta^{18}O$ *record from the GRIP ice core, total diatom accumulation rate (DAR), first principle component of the planktonic community, time series of key diatom species* Puncticulata radiosa *and proportion of planktonic and periphytic taxa (%) from Kälksjön, redrawn from Randsalu-Wendrup et al. 2012 (Paper I).* $\mathit{DAR}_{\mathit{total}}$ *and PCA1 of the planktonic community were analysed for change-points over time according to details in Paper I. The optimal change-point model is shown with solid lines, and the alternative less suitable model with dashed lines.*

6. Regime shifts in response to abrupt climate cooling

One manifestation of abrupt climate cooling (and subsequent warming) is the ”8.2 ka cooling event”, assumed to be the highest magnitude climate change of the Holocene in the northern mid- to high latitudes (Daley et al. 2011). Analysis of Greenland ice-core records indicates that an abrupt cooling event began around 8175-30 cal. yr BP and lasted for *c.* 150 years, with maximum cooling of approximately 3° lasting *c.* 70 years (Kobashi et al. 2007). The event is believed to have been caused by the injection of glacial melt-water from ice-dammed Lake Agassiz-Ojibway into the Labrador Sea (e.g. Clarke et al. 2004; LeGrande et al. 2006; Wiersma & Renssen 2006; Daley et al. 2011), slowing down the ocean thermohaline circulation (THC) and its associated heat transport (e.g. Alley et al. 1997; Barber et al. 1999; Wiersma & Renssen 2006) and leading to a pronounced short-lived cooling in the North

Atlantic region (Wiersma & Renssen 2006; Daley et al. 2011). A cooling episode around 8200 cal. yr BP has been described in several proxy records in the Northern Hemisphere (e.g. Alley et al. 1997; Tinner & Lotter 2001; Veski et al. 2004; Hammarlund et al. 2005; Ojala et al. 2008; Panizzo et al. 2008; Snowball et al. 2010), and in Paper I we investigate a detailed diatom record from Lake Kälksjön, west-central Sweden, for signs of ecological regime shifts in response to the event. We find that the lake displayed two distinct periods of abrupt ecological change during the investigated time period (8500-7500 cal. yr BP): a change in diatom accumulation rate at *c.* 8040 cal. yr BP and a shift from periphytic to planktonic dominance at *c.* 7850 cal. yr BP (Fig. 10). The first shift is an abrupt step change with a doubling of diatom accumulation rates over a period of 5-10 years, which can be connected to a sudden change in precipitation leading to increasing erosion in the catchment and a rapid increase in nutrients entering the lake. The regime shift in the driver (increased precipitation/erosion/nutrients) was linearly mediated to the ecosystem state, and the shift can be classified as type I – smooth regime shift. The second shift is more complex and connected to the gradual climate warming following the 8.2 ka event. The warming led to stable lake stratification, a shallower mixing depth, a shift to dominance of planktonic species and an abrupt shift within the planktonic community over 5-10 years at *c.* 7850 cal. yr BP, from taxa indicative of cold conditions to increased importance of small *Cyclotella* spp. We classify this as a type II – threshold like regime shift, where the change in driver (climate warming) did not seem to affect the planktonic community until a critical threshold was reached, at which point the system state changed rapidly.

The reaction of Lake Kälksjön to the 8.2 ka cooling is not as pronounced as the reaction to the following warming: a prolongation of the early, postglacial, Fragilariaceae dominated conditions occurred, and planktonic diatom composition changed abruptly to taxa more tolerant of cold conditions, weak stratification and deep water-column mixing in the summer months (e.g. *Puncticulata radiosa*). This reaction differs from the reaction of many Fennoscandian lakes to the cooling: Lake Nautajärvi in southern central Finland, for example, showed a shift from a planktonic species dominance to more littoral species dominance around 8160 cal. yr BP (Ojala et al. 2008), and in small west Greenland Lake SS2, an abrupt shift from a planktonic to a periphytic community, including the sudden disappearance of *Puncticulata radiosa*, took place at the same time (Anderson et al. 2008).

The differential response of lakes in different locations reveals the role of local conditions, such as vegetation and morphometry, in mediating the nature of limnological response to a given environmental forcing. In order to further investigate the ecological significance of the 8.2 ka cooling event, palaeolimnological diatom records (and one pigment record) from 14 sites, ranging from mid-latitude to high-latitude, covering the time period 9000-7000 cal. yr BP (Table 2; Fig 11) were examined. Since the records are characterized by coarse and varying time resolution, it is difficult to distinguish between a gradual smooth trend and abrupt shifts. The method of Zeileis et al. (2003), which identifies thresholds in time separating several distinct stationary periods, but which will also identify several thresholds during non-stationary periods with increasing or decreasing trends, was used. In order to reduce the number of variables to be analysed for regime shifts, and to analyse changes in diatom communities rather than individual species, the first four principle components of the diatom and pigment data were analysed for thresholds. We defined a window of size 2k observations with k observations on each side of the supposed threshold and calculated the likelihood ratio (LR) test statistic for a difference in mean between the two groups. The LR test statistic was calculated for n-2k+1 sliding windows through the time series of n observations, with high values indicative of a threshold. The size of the window was chosen to be sufficiently small relative to the length and resolution of the time series (k=3-5) to allow for assuming almost unchanging conditions within each of the two groups of observations. The critical values of the LR test were found simulating a normal random process, corresponding to the null hypothesis, and finding the maximum of all sequential LR test statistics. This simulation was repeated 10,000 times, and the 95-percentile of this simulated maximum LR test statistic distribution provided an estimated critical value for the proposed LR test statistic on a 95% confidence level. Test

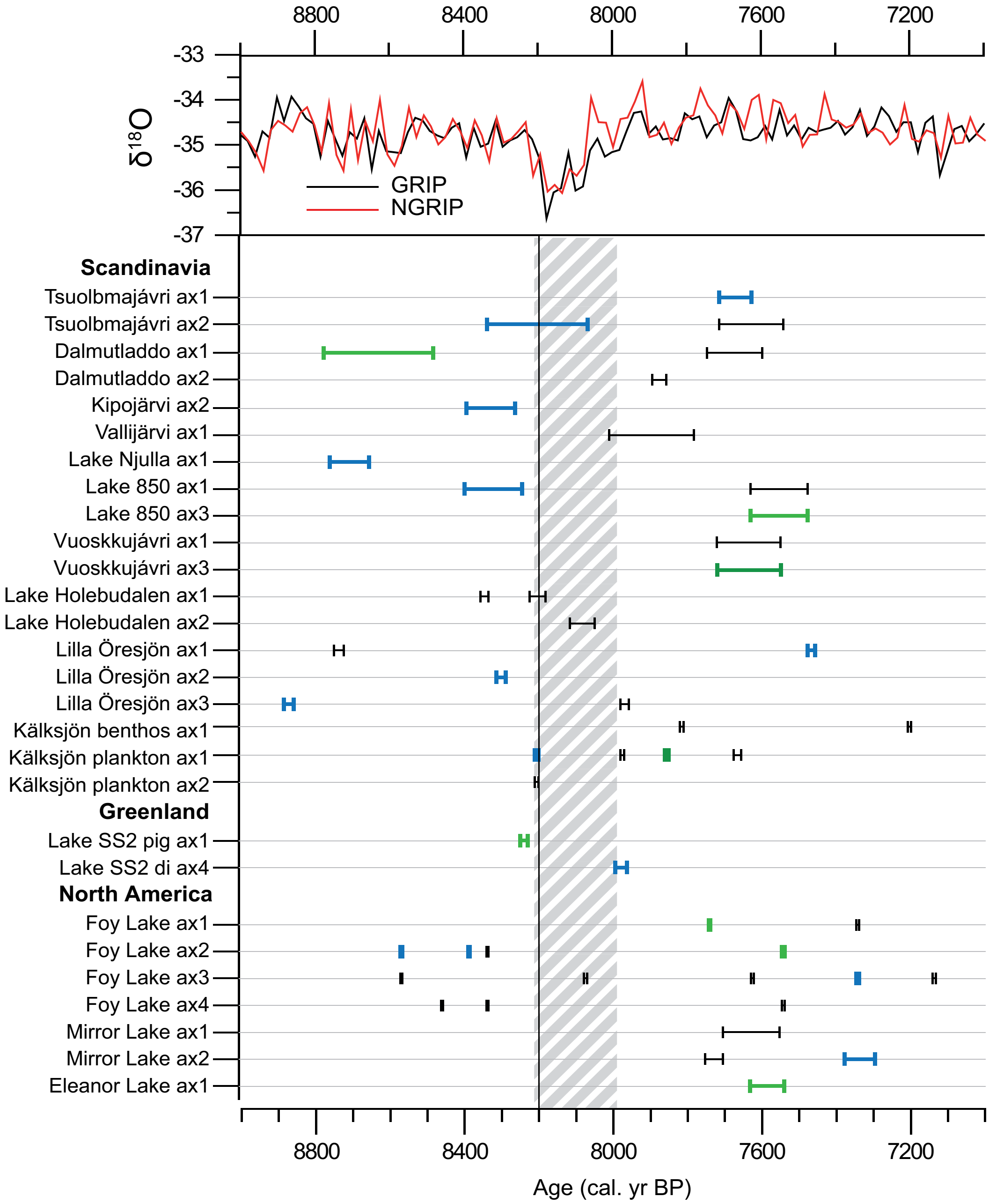

Figure 11. Statistical overview of the 8.2 ka event with breakpoints of individual variables (PCA-axes) based on LR statistics, and $\delta^{18}O$ records from the GRIP and NorthGRIP ice-cores. Hatched area indicates the 8.2 ka event as described by Kobashi et al. (2007), vertical line = 8200 cal. yr BP. Error bars indicate the time steps of the original record around the breakpoint. All shown breakpoints are significant at $p<0.05$, while blue indicates significant at $p<0.01$ and green significant at $p<0.001$.

statistics exceeding this critical value were identified for all analysed principle components and compared for commonalities in the detected thresholds and with climate records from the Greenland ice cores (Fig. 11). The statistical analysis shows that there are several significant breakpoints around the 8.2 ka event and also around 7600 cal. yr BP, possibly linked to a proposed *c.* 4.5 m abrupt rise in eustatic sea level caused by a large meltwater pulse from the decaying Laurentide ice sheet (e.g. Yu et al. 2007; Törnqvist and Hijma 2012), but the results are not striking.

Lake Holebudalen, Lake SS2, Lake Kälksjön and possibly Lake Lilla Öresjön have the highest resolution records and are the lakes that show abrupt shifts around 8200 cal. yr BP (Fig 11). At Holebudalen there was a rapid shift from tychoplanktonic to benthic diatom dominance at

Table 2: Overview and test statistics of lakes included in the analysis of the 8.2 ka event. All breakpoints are significant at $p<0.05$, while $^{*}p<0.01$, $^{**}p<0.001$.

Lake	Variable	# obs	# obs on each side	Breakpoint	LR statistic	Critical value	References
Tsuolbmajávri	Diatom axis 1	23	5	7629-7716	15.16*	10.97	Seppä & Weckström (1999), Korhola et al. (2000)
	Diatom axis 2	23	5	7543-7716	12.69, 13.04	10.97	
				8069-8340	12.17, 19.68, 11.53*		
Dalmutladdo	Diatom axis 1	17	5	7600-7748	11.97	9.51	Unpublished
				8485-8780	13.84, 19.41**		
	Diatom axis 2	17	5	7858-7895	11.50		
Kipojärvi	Diatom axis 2	15	4	8265-8396	15.06*	10.13	Unpublished
Vallijärvi	Diatom axis 1	9	3	7783-8012	12.55	10.19	Unpublished
Lake Njulla	Diatom axis 1	11	3	8657-8763	16.24*	11.45	Bigler et al. (2003)
Lake 850	Diatom axis 1	13	4	7478-7631	11.12	9.71	Bigler and Hall (2003)
		13	4	8246-8400	17.99*		
	Diatom axis 3	13	4	7478-7631	18.85**		
Vuoskkujávri	Diatom axis 1	12	4	7551-7723	11.12	9.31	Bigler et al. (2002)
	Diatom axis 3	12	4	7551-7723	18.85**		
Lake Holebudalen	Diatom axis 1	40	5	8183-8226	15.89, 16.12	12.83	Panizzo et al. (2008)
		40	5	8336-8358	17.10		
	Diatom axis 2	40	5	8051-8117	14.34, 11.10, 14.25		
Lilla Öresjön	Diatom axis 1	88	5	7458-7478	19.92*	15.26	Renberg (1990b)
		88	5	8725-8752	16.21		
	Diatom axis 2	88	5	8290-8315	19.46*		
	Diatom axis 3	88	5	7958-7981	17.58		
		88	5	8860-8887	19.10*		
Kälksjön	Periphyton axis 1	78	5	7811-7821	16.66	~15	Randsalu-Wendrup et al. (2012)
		78	5	7200-7208	17.61		
	Plankton axis 1	78	5	7656-7676	15.39		
		78	5	7851-7861	25.36**		
		78	5	7971-7981	15.34		
		78	5	8201-8211	20.55*		
	Plankton axis 2	78	5	8201-8211	18.67		
Lake SS2	Pigment axis 1	46	5	8230-8251	26.92**	13.22	Anderson et al. (2008)
	Diatom axis 4	18	5	7964-7995	14.23*	9.85	
Foy Lake	Diatom axis 1	271	5	7339-7347	21.23	18.34	Stone and Fritz (2006)
		271	5	7739-7743	48.43**		
	Diatom axis 2	271	5	7539-7547	28.12**		
		271	5	8336-8341	19.97		
		271	5	8387-8392	24.15*		
		271	5	8568-8573	23.93*		
	Diatom axis 3	271	5	7133-7141	21.26		
		271	5	7339-7347	23.44*		
		271	5	7622-7630	19.39		
		271	5	8071-8080	21.51, 20.89		
		271	5	8568-8573	19.34		
	Diatom axis 4	271	5	7539-7547	19.53		
		271	5	8336-8341	18.68		
		271	5	8458-8463	21.23		
Mirror Lake	Diatom axis 1	30	5	7553-7705	14.66	11.84	Unpublished
	Diatom axis 2	30	5	7296-7378	20.40*		
Eleanor Lake	Diatom axis 1	16	5	7540-7632	12.84, 22.02**	9.22	Unpublished

c. 8225 cal. yr BP, SS2 had a major reduction in lake productivity and changed algal community composition around 8200 cal. yr BP, and in Lilla Öresjön the disappearance of planktonic *Cyclotella* species occurred around the same time. Although these are high-resolution records, significant dating problems make it all but impossible to unambiguously correlate the observed changes to the 8.2 ka event as described from Greenland ice cores. The chronology of Lilla Öresjön is based on one radiocarbon date at 7800 BP and the knowledge that the lake was formed after deglaciation about 12,600 years ago (Renberg 1990b), and both Holebudalen and SS2 have chronologies based on dates obtained on bulk sediment samples. Hard-water effects, which are not only confined to lakes with carbonates in their catchments, are usually more pronounced shortly after deglaciation, but, as demonstrated by Barnekow et al. (1998), substantial deviations between dates obtained on macroscopic terrestrial plant remains and bulk sediment may persist throughout the Holocene. Some of the other Scandinavian records (Lakes Tsuolbmajavri, Kipojärvi and 850) showed shifts at or slightly before 8200 cal. yr BP, but all of these lakes have records that are so poorly resolved (150-300 years/sample) that they cannot be clearly linked to the 8.2 ka event, and the ecosystem response to the short-lived cooling event may well be hidden in the time integration inherent to sediment records. The lack of response to the 8.2 ka event in well-dated and highly resolved Foy Lake, as well as the other North American lakes, is not surprising, as the event is mainly thought to have affected the North Atlantic region (e.g. Alley et al. 1997; Shuman et al. 2009).

The results of our analyses highlight the need for high sampling resolution and precise chronological control when trying to detect, quantify and test for regime shifts in response to rapid climate change. This small study also emphasises the point we make in Paper III that the strength of palaeolimnology, especially when dealing with chronological uncertainties, might not be to look directly at individual changes, but to be able to use long sediment records to evaluate the mean state and natural variability of a lake ecosystem throughout its history.

7. Regime shifts and alternative stable states in a shallow lake

Bistable regime shifts with hysteresis are especially well documented in shallow lakes, often in association with anthropogenic eutrophication (e.g. McGowan et al. 2005; Hargeby et al. 2007; Scheffer and Jeppesen 2007; Scheffer and van Nes 2007; Zimmer et al. 2009; Sayer et al. 2010a; Hobbs et al. 2012). The deterioration of shallow lakes from a clear-water, macrophyte-dominated regime to a turbid, phytoplankton-dominated regime has been described theoretically by, for example, Scheffer et al. (1993) who, in this rather iconic paper, used Krankesjön as an example. Theory predicts that increasing nutrient conditions decreases the stability of the clear-water regime until a critical threshold is reached, at which time the lake shifts to a turbid regime. Re-establishment of the clear-water regime is not possible unless nutrient concentrations are significantly reduced, and the system displays hysteresis (Scheffer et al. 2001; Box 1). Both states are thus dependent on self-stabilizing mechanisms, with submerged macrophytes increasing water clarity, thereby enhancing their own growing conditions through reduction of nutrients in the water column, protection of phytoplankton grazers against fish predation, and prevention of sediment resuspension. Fish in turn maintain the turbid state through resuspension of sediments and by controlling the phytoplankton grazers, allowing the phytoplankton to flourish (Scheffer et al. 2001). An external perturbation can cause a regime shift in the lake at moderate nutrient levels, but at low and high nutrient concentrations clear and turbid regimes are the only possible states (Scheffer et al. 1993; Scheffer and Carpenter 2003).

Krankesjön has a history of regime shifts documented for almost a century as summarized in Paper II and Figure 8. The reasons behind the shifts are, however, not well understood, despite extensive study of the lake. High water levels, enhanced wave action and erosion due to winters without ice cover, high nutrient levels and high fish biomass have been suggested as possible forces behind the shifts to the turbid state, while low water levels, reduction of fish densities due to disease and lower nutrient levels have been put forward as forces initiating the clear water

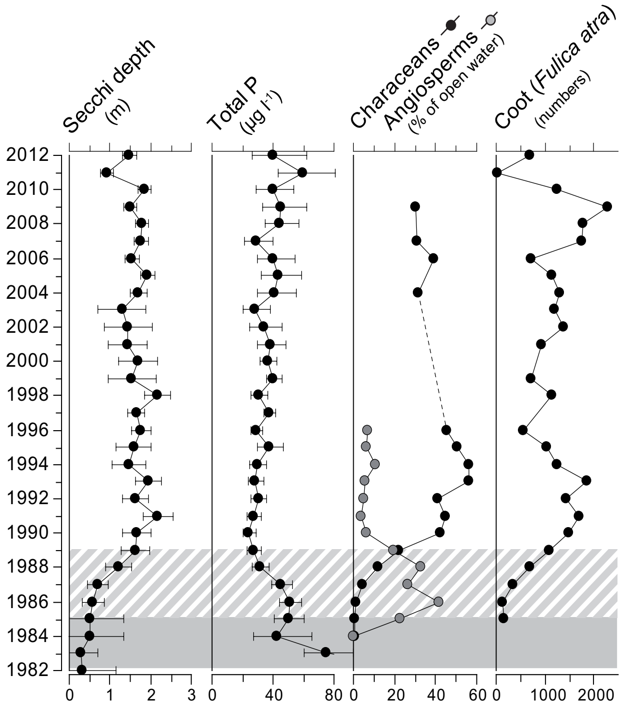

Figure 12. Yearly means (Mar-Sep) of Secchi depth and total phosphorus data from Krankesjön along with macrophyte cover (%) and october-november mean numbers of coot (Fulica atra). Macrophyte cover data from Nicolle (2010), bird data from H Källander, L-A Hansson (personal communication, unpublished data). Grey shading indicates turbid conditions and dashed shading intermediate conditions. Error bars mark the 95% confidence interval of the mean.

state (Karlsson et al. 1976, Blindow 1992, Blindow et al. 1993, Hansson et al. 2007, Hargeby et al. 2007, Brönmark et al. 2010). In Paper II we find that the historically described and previously investigated regime shifts from clear to turbid conditions in 1975 and turbid to clear conditions in the mid-1980s are apparent in the monitoring data and visible, but less clearly recorded, in the palaeolimnological data. The shift to turbid conditions in 1975 was registered as a rapid decrease in Secchi depth, an increase in turbidity and increases in total nitrogen and phosphorus concentrations. In the sediment record a brief increase in diatom productivity followed by a likely shift in dominance from diatoms to cyanobacteria and green algae occurred during the remainder of the turbid state. A feasible explanation for the shift is reduced resilience of the ecosystem due to eutrophication, combined with extremely high spring water levels in 1975 leading to die-off of submerged macrophytes. The shift back to the clear-water state in the late 1980s was more gradual, with Secchi depth increasing and turbidity decreasing over a period of 4-5 years, starting in 1985 when macrophytes were re-established in the lake (Fig. 12). A suggested explanation for their return is the kill-off of bream population (*Abramis brama*), a bottom feeding fish that prevents colonisation of submerged vegetation (ten Winkel and Meulemans 1984), due to disease in late spring 1985 and 1986. This shift is not easily identified in the sediment record, and it appears that the ecosystem changed to a different clear-water state than that prior to the collapse (Fig. 13). Within the diatom community a shift occurred around 1978, when cyanobacteria and green algae were the dominant primary producers, and diatom production rates were low. The shift can be connected to the disappearance of submerged macrophytes, but the two diatom community regimes appear to be ecologically synonymous in that they could occur under similar settings. Thus, as water clarity improved and diatom production increased, the new diatom community persisted into the clear-water state (Fig. 13).

The use of palaeolimnological data in combination with monitoring data provides insights into components of the ecosystem that were not measured in contemporary surveys and that were stable, despite shifting water clarity and macrophyte cover. The reaction of Krankesjön to shifting conditions is complex and non-linear, and it is possible that the lake is not as good an example of alternative stable states as has been previously assumed (e.g. Scheffer et al. 1993). There are, in fact, suggestions that the shifts between turbid and clear water states in shallow lakes in general are gradual and not necessarily sudden processes at all.

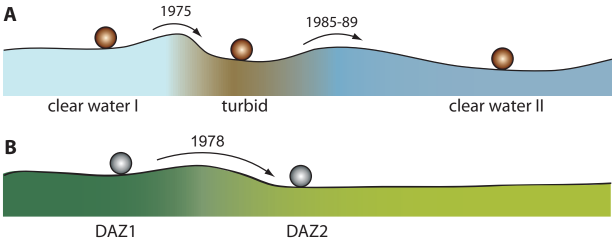

Figure 13. Schematic of regime shifts in Krankesjön in (a) lake water clarity (b) diatom community composition. DAZ 1 and DAZ 2 refer to diatom accumulation zones in Paper II.

Scheffer and van Nes (2007) argue that there is no single critical nutrient level for maintaining a clear-water state, as factors such as lake size, depth and climate affect the threshold. They conclude that the change of lake communities along a gradient of eutrophication may be regarded as a continuum in which gradual species replacements are interrupted at critical points by moderate or dramatic shifts to contrasting community states (Scheffer and van Nes 2007). Sayer et al. (2010a; 2010b) hypothesised a slow-enacting (10-100's years) feedback loop in nutrient-enriched shallow lakes, where long-term losses of macrophyte species (due to eutrophication) lead to reduced periods of plant dominance. This may then afford increased seasonal opportunities for phytoplankton development, placing greater pressure on remaining macrophytes, thus edging the lake towards phytoplankton dominance (Sayer et al. 2010a). van Nes et al. (2007) propose a theory for cyclic shifts between alternative states in some shallow lakes, where submerged plants create a positive feedback on their own growth by clearing the water but in the long run undermine their position by increasing nutrient retention and creating a slow ”internal eutrophication”. This results in periods of low resilience, when even a weak disturbance can trigger a shift to the turbid state. Hargeby et al. (2007) argue that this kind of behaviour may be a factor behind the shifts in Krankesjön and could explain the difficulties in identifying the specific causes behind the shifts in the lake.

Krankesjön has remained in the clear-water state since the late 1980s, although mean Secchi depth has varied more than a meter (Fig 12). It appears that the water clarity (represented by Secchi depth) at which submerged vegetation came to dominate the lake in the mid-1980s was higher than the water clarities that have occurred later during the clear water state, suggesting that the system exhibits hysteresis, with macrophyte cover remaining extensive enough to maintain feedback mechanisms for water clarity (Nicolle 2010). In recent years, however, the system seems to be changing with increasing phosphorus levels and lower abundance of characeans (H. Källander, personal communication; Fig. 12). This suggests increasing instability and lower resilience of the clear water conditions (possibly due to cyclic behaviour as suggested by Hargeby et al. (2007)), meaning that the possibility for a shift to turbid conditions has increased. This is consistent with reports of periods of instability of the clear water state in 1997 and 1999 (Blindow et al. 2002) and most recently during 2011-2012 (C. Brönmark and L-A. Hansson, unpublished data), also reflected in unusually low numbers of coot (*Fulica atra*), a herbivorous waterfowl which can be used as a rough indication of macrophyte cover (Hansson et al. 2010; H. Källander, personal communication, unpublished data; Fig. 12).

A prospective future prospect is to continue the cooperation between aquatic ecologists and palaeoecologists on Krankesjön and synthesize additional contemporary data (on fish, water chemistry, macrophyte dynamics, etc) with extended palaeolimnological records back to pre-disturbance time. This could establish natural lake variability and lake state and shed light on whether the recent shifts between clear-water and turbid conditions are anomalies or part of a natural cyclic behaviour of the lake. This would require additional proxies, such as plant macrofossils and zooplankton remains, as well as well-dated records, which might be a challenge, because the lake is calcareous and terrestrial macrofossils in the sediments are precious few.

8. Conclusions

- Regime shifts in lake ecosystems can occur with both abrupt and continuous climate change, and they may leave an imprint in palaeolimnological records, allowing for the investigation of patterns and processes governing abrupt ecological changes on geological timescales. In this thesis I demonstrate that not only can regime shifts be detected in sediment records, they can also be quantified and statistically tested for using, for example, change-point models. A key element for rigorous quantitative methods, however, is high sampling resolution and precise chronological control. Thus, in order to further our understanding of regime shifts in lake ecosystems in general, and in palaeolimnological records in particular, more well-dated high-resolution sediment records are needed, especially spanning time periods of known climate change, such as the Medieval Climate Anomaly and the Little Ice Age.

- When detected, past regime shifts and palaeolimnological records offer rich opportunities to increase the understanding of ecosystem responses to climate changes and to evaluate the mean state and natural variability of lake ecosystems on timescales of decades to millennia. Palaeolimnological archives provide a perspective on whether the pre-disturbance ”natural” state that may be the target of restoration efforts is in fact natural, or if it is an anomaly in lake history, and if this target is at all possible to reach or if it, due to shifting baselines and lake ontogeny, is no longer a realistic restoration endpoint.
- Linking the timescales of contemporary ecology with palaeoecology/limnology may provide long-term records of lake history and opportunities to further disentangle the role of different forcings on lake ecosystems. An improved understanding of lake ecosystem dynamics and regime shifts in lakes through the cooperation of limnologists/ecologists and palaeolimnologists may better prepare us to face future climate change and to fully understand and perhaps mitigate the effects of global climate change on lake ecosystems.

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◆

Svensk sammanfattning

Paleolimnologiska undersökningar av regimskiften orsakade av klimatförändringar

- **Paleolimnologi:** vetenskapen om sjöars ekologiska förhållanden genom historien (paleo - gammal, limnologi - vetenskapen om inlandsvattnens ekologi)
- **Regimskifte:** ett abrupt och varaktigt skifte från en typ av ekosystem till ett annat
- **Tröskel, tröskelvärde:** den tidpunkt vid vilket detta abrupta skifte sker; där en liten förändring i yttre påverkan (t.ex. klimat, näringstillförsel) kan leda till en stor ekosystemförändring (droppen får bägaren att rinna över)

Traditionellt sett har man tänkt sig att gradvisa förändringar i yttre miljöfaktorer leder till lika gradvisa ekosystemförändringar, men vi vet nu att ekosystem som utsätts för mänsklig påverkan eller klimatförändringar kan reagera kraftigt och abrupt genom att ett ekologiskt tröskelvärde överskrids varvid en förändring sker från en stabil ekologisk situation till en annan. Dessa snabba förändringar kallas för regimskiften och konceptet används inom bland annat ekologi, klimatforskning, ekonomi och medicin.

Sjöar är känsliga för klimat- och miljöförändringar och ända sedan de bildades avsätts sediment på botten. Dessa sediment består av en blandning av material från sjöns omgivning, föroreningar från atmosfären och material som bildas i sjön, och lagerföljden av bottensediment i varje sjö utgör därmed ett historiskt arkiv över sjön och dess omgivning. Genom att studera sjösediment kan man därmed undersöka hur sjöars tillstånd har varierat genom historien och få inblick i såväl gångna tiders klimat- och miljöförändringar, som information om hur sjöars ekosystem påverkats av dessa förändringar. Kopplingen mellan en sjös ekosystem och yttre miljöpåverkan är dock mycket komplex och alla de faktorer som påverkar sjön (klimat, mänsklig påverkan, interna processer, dräneringsområde) interagerar med varandra, varierar i tid och rum och påverkar såväl ekosystemen direkt som filtrerar de klimatsignaler som når sjön. Detta innebär att liknande sjöar kommer att reagera olika på samma slags yttre påverkan, samt att en enskild sjö kommer att uppvisa olika slags reaktioner vid olika tidpunkter.

I denna avhandling undersöker jag om och hur man kan se spår av regimskiften i sjösediment och försöker genom detta utöka vår förståelse för vilka yttre processer som kan leda till skiften, samt hur dessa regimskiften kan yttra sig. Jag har framför allt analyserat kiselalger (även kallade diatoméer): encelliga organismer som bildar svårnedbrytbara skal av kiseldioxid som bevaras bra i sedimenten. Artsammansättningen i diatomésamhället styrs av förhållandena i sjön och genom att artbestämma och räkna de alger som finns bevarade i sedimenten kan jag dra slutsatser om hur förhållandena varierat under tidigare perioder i en sjös historia. Jag har dels undersökt två svenska sjöar: Kälksjön i Värmland (artikel 1) och Krankesjön i Skåne (artikel 2), dels sammanfattat sentida paleolimnologiska forskningsresultat där sjöar uppvisat regimskiften (artikel 3).

I artikel 3 beskriver vi tre typer av regimskiften, enligt vilka vi klassificerar de exempel vi undersökt (se figur 2):

- **Typ I:** jämna skiften där en plötslig yttre förändring leder till en lika plötslig ekosystemförändring
- **Typ II:** tröskel-lika skiften där en successiv yttre förändring inte påverkar ekosystemet synbart förrän ett tröskelvärde överskrids varvid ekosystemet plötsligt förändras.
- **Typ III:** bistabila skiften med omväxlande jämviktslägen. Dessa skiften liknar typ II, men när systemet väl skiftat kommer en omkastning av den yttre förändringen inte att leda till att systemet följer samma kurva och skiftar tillbaka. Ett exempel på detta är grunda sjöar som något förenklat kan ha antingen klart eller grumligt vatten. När näringstillförseln till en klarvattensjö ökar påverkas den inte förrän en viss näringsnivå uppnås varvid sjön plötsligt skiftar och blir grumlig. När den väl är grumlig håller den sig dock i det läget och för att återgå till klart vatten räcker det inte att minska näringstillförseln till den nivå varvid sjön skiftade sist, utan man måste minska den ytterligare för att uppnå ett skifte tillbaka. Detta beror på att olika återkopplingsmekanismer vidmakthåller den regim, eller det läge, som sjön befinner sig i (klart respektive grumligt vatten).

Utöver denna klassifikation av regimskiften har vi också urskilt sex olika typer av påverkan som kan leda till regimskiften i sjöar:

- klimatpåverkan – isdynamik (under hur lång tid sjön är täckt av is påverkar ljusförhållanden, växters tillväxtsäsong med mera)
- klimatpåverkan – nederbörd (kan förändra sjöns vattenstånd samt vattenkemi)
- klimatpåverkan – cirkulation och stagnation (påverkar levnadsförhållandena för organismer samt näringshalten i sjön)
- klimatpåverkan – dräneringsområdets vegetation (påverkar näringstillförsel, vind, erosion med mera)
- ontogeni – sjöns naturliga utveckling (ackumulation av sediment leder till grundare vatten, många sjöar upplever en naturlig försurning)
- mänsklig påverkan – avskogning, föroreningar, övergödning

I artikel 3 kombinerar vi detta genom att undersöka sambanden mellan typ av påverkan och typ av regimskifte.

Artikel 1 beskriver vår undersökning av Kälksjön i Värmland. Denna sjö är varvig, eller årslaminerad, och genom att räkna de individuella varven och kombinera detta med kol-14-datering har en kontinuerlig kronologi med hög precision och tidsupplösning skapats. Vi har undersökt sediment från 7500 till 8500 år före nutid (nutid = 1950 vid kol-14-datering) med fokus på förändringar av diatoméernas artsammansättning, för att se hur en kort period med kallare klimat 8200 år före nutid (*8.2 ka cooling event*) påverkade sjöns ekosystem, samt undersöka om denna period gav upphov till regimskiften i sjön. Vi fann ett regimskifte ca 8040 år före nutid då produktiviteten fördubblades över 5-10 år, antagligen på grund av kraftig nederbörd vilket ledde till ökad erosion och med det ökad näringstillförsel till sjön. Detta regimskifte klassificerar vi som typ I där plötslig yttre påverkan (kraftig nederbörd) ledde till en lika plötslig ekosystemförändring (ökad produktivitet). Ett annat skifte skedde som respons på att klimatet återigen blev varmare, men detta skifte är av typ II: sjön påverkades inte av uppvärmningen förrän ett tröskelvärde överskreds runt 7850 år före nutid då diatomésamhället plötsligt förändrades kraftigt. Sammanfattningsvis är studien ett exempel på att man kan spåra, mäta, statistiskt säkerställa och kvantifiera regimskiften i sedimentdata, men att det kräver sediment med hög tidsupplösning och hög dateringsprecision.

I artikel 2 har vi undersökt Krankesjön utanför Lund och jämfört sedimentdata med ekologisk mätdata som finns insamlad sedan sent 1960-tal. Krankesjön är en grund fågelsjö med Natura 2000-status, som skiftat mellan klart och grumligt vatten ett par gånger under de senaste 100 åren, men trots intensiva studier har mekanismerna bakom skiftena inte klarlagts. Vi inriktade oss på sjöns senaste skiften från klart till grumligt vatten 1975 och tillbaka till klart vatten i slutet av 80-talet och fann att vi kunde spåra dessa skiften i sedimenten. Resultaten var dock inte helt entydiga: diatomésamhället påverkades till exempel inte synbart av vattenkvaliteten utan skiftade först 1978 till ett samhälle som fortlever intill denna dag. De slutsatser vi drar av denna undersökning är att dessa skiften från klart till grumligt vatten kanske inte är exempel på omväxlande jämviktslägen som tidigare antagits, utan att sjön, förutom att påverkas av yttre faktorer, eventuellt även uppvisar ett naturligt och komplext cykliskt beteende. De senaste åren har Krankesjön verkat vara på väg att återigen skifta till grumligt vatten och då detta är till nackdel för sjöns status som fågelsjö vill Länsstyrelsen vidta åtgärder för att förhindra ett sådant skifte. Vår undersökning bidrar med viktig bakgrundsinformation för planering av sådana åtgärder.

I min avhandling visar jag att klimatförändringar och mänsklig påverkan har orsakat regimskiften i sjöar genom historien samt att man, genom att använda väldaterade och högupplösta sedimentarkiv kan spåra och undersöka dessa skiften. I och med EUs vattendirektiv har Sverige åtagit sig att uppnå god status i alla vatten innan år 2016 och god status definieras som inga eller mycket små avvikelser från opåverkade förhållanden. Men vad är opåverkade förhållanden? Dagens miljötillstånd är ju resultatet dels av naturens egna långsiktiga dynamik, dels av människans påverkan under flera tusen år och vilket tillstånd sjöar som är påverkade av försurning eller övergödning ska återställas till är en komplicerad fråga. Genom att kombinera nutida mätdata med sedimentdata kan man få tillgång till långa historiska arkiv och för att verkligen förstå sjöars utveckling och tillstånd krävs att paleolimnologer och ekologer/limnologer samarbetar. Sådana samarbeten kan hjälpa till att sätta realistiska mål för åtgärdsprogram samt hjälpa oss att förstå, samt kanske förmildra, den påverkan som global uppvärmning kommer att ha på sjöars ekosystem i framtiden.

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