

Paleolimnological records of regime shifts in lakes in response to climate change and anthropogenic activities

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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 paleolimnological records allow us to investigate and better understand patterns and processes governing ecological changes on geological time scales. This synthesis investigates paleolimnological records that display apparent regime shifts and characterizes the shifts as either smooth, threshold-like or bistable. The main drivers behind the shifts are also explored: 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 leaves in sediment

records. Our analysis of the limited sites available (22 sites) show that smooth regime shifts are characterized with forcing and response variables acting on similar time scales, whereas regime shifts that demonstrate a threshold like response or a hysteresis response occur on shorter time scales than changes in drivers. The temporal resolution of the record, a common concern in paleo records, limits identification of the timing and rate of the regime shifts. When detected, past regime shifts offer rich opportunities to understand ecosystem responses to climate and other changes and to evaluate the mean state and natural variability of lake ecosystems on time scales of decades to millennia. There are a number of remaining challenges in understanding regime shifts and ecosystem dynamics in a paleolimnological perspective including lack of an appropriate temporal resolution and ecosystem feedback mechanisms. Combining paleoecology with contemporary studies can help clarify the scale of regime shifts and to distinguish patterns in ecosystem changes from natural variability.

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Introduction

Much of the research on regime shifts in the geological literature has had a paleoclimatic 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. The theoretical model of abrupt ecosystem change in response to a small and/or a continuous change in forcing has been around for about 40 years (Holling 1973; Noy-Meir 1975; May 1977). Although the terminology is varied (tipping points, regime shifts, critical transitions, bifurcations, etc.), 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. 2001b; Scheffer and Carpenter 2003; Folke et al. 2004; Andersen et al. 2009; Williams et al. 2011).

In this synthesis we investigate regime shifts in paleolimnological records and characterize them based on a framework described in Andersen et al. (2009), while also exploring the likely physical processes driving the shift. Although varied physical processes interact, such that there may not be a single driver of any observed change, this framework may elucidate the relationship between driver and regime shift dynamics and the associated imprint of a regime shift in the sediment record. When detected, past regime shifts offer rich opportunities to understand ecosystem responses to climate changes and the natural state and variability of ecosystems undergoing restoration efforts.

Framework

The terminology regarding regime shifts and regime shift theory has varied, and there is still no clear consensus on definitions and terminology. For the purpose of this paper, the significant terms are defined 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 a threshold is key for demonstrating bistability or hysteresis according to Andersen et al. (2009). The existence of a threshold does not, however, always entail a regime shift; the state crossed into might not be persistent (Dodds et al. 2010).

Andersen et al. (2009) describe three scenarios for, or types of, regime shifts that we use as the base of our characterization (Fig. 1):

Type I “Smooth” pressure-status relationships, where an abrupt shift in the driver (e.g. climate change or nutrient input) is directly mediated to the ecosystem state.

Type II Threshold-like state responses, where an ecosystem undergoes a regime shift only after the driver exceeds a threshold; the relationship between the forcing and the response variables is non-linear.

Type III Bistable systems, which exhibit hysteresis behavior with two alternative regimes during increasing and decreasing modes of the driver.

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 ecosystems are complex, the threshold at which a regime shift occurs, as well as the degree of reversibility, depends on the resilience or the strength of the feedback mechanisms maintaining the current state. This is usually determined by multiple factors, such as the composition of the biological community, lake depth and morphometry. Therefore ecosystem responses to the same forcing will differ among different systems and might also change over time within the same system: the same lake may display

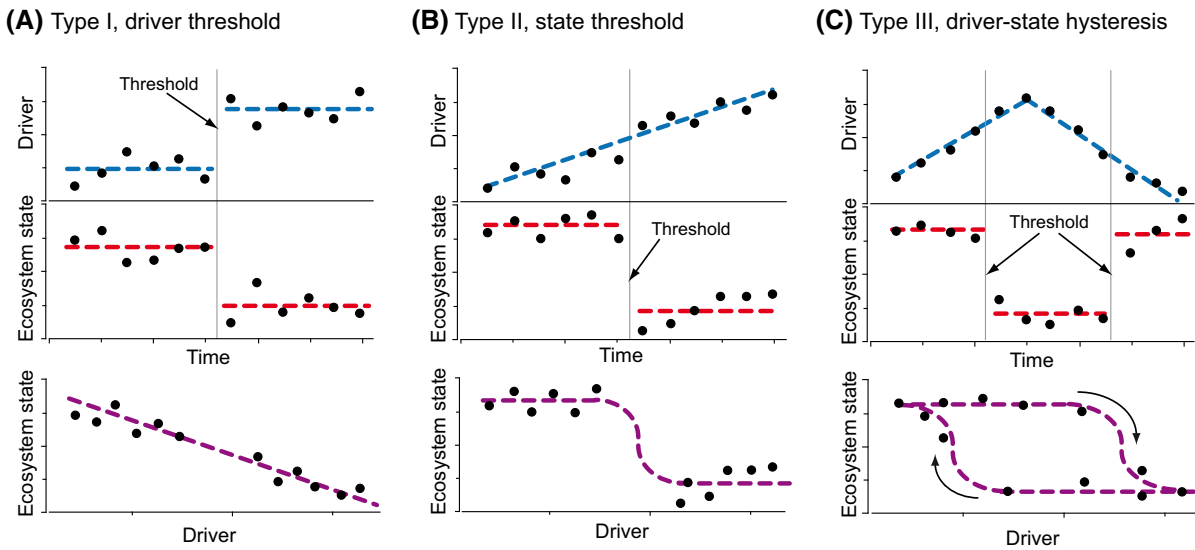


Fig. 1 Three types of regime shifts. The *two top rows* show time series of driver (e.g. nutrient input) and ecosystem state (e.g. macrophyte cover), and the *lower row* shows the relationship between driver and ecosystem state. *Grey vertical lines* represent regime shifts. **a** Type I: smooth pressure-status 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 and 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)

linear or hysteretic responses depending on local conditions (Crépin et al. 2012). It is also possible that, during the time spent in one state, changes in forcing (for example CO₂ concentration, temperature, wind patterns, lake infilling) may preclude the system from returning to previous conditions (Duarte et al. 2009).

While lakes are outstanding sentinels of environmental and climate change (Battarbee 2000; Williamson et al. 2009; Adrian et al. 2009; Leavitt et al. 2009), climate change impacts are often complex and multi-faceted, because the climatic signal is filtered through both catchment and in-lake processes. Thus, the structure and function of lake ecosystems is determined by complex interactions between climate change, humans, in-lake processes, lake ontogeny and catchment features (geology, soils, vegetation). Each of these variables varies in time and space and may have considerable influence on biological structure, as well as act as information filters, thereby altering climate effects on lakes (Schindler et al. 2001; Anderson et al. 2004; Leavitt et al. 2009; Fritz and Anderson 2013). We have identified three main driver pathways leading to regime shifts: (1) climate

(including ice cover, precipitation, mixing and stratification, and catchment vegetation), (2) lake ontogeny (long-term changes in the lake or catchment associated with successional processes), and (3) anthropogenic forcing (including deforestation, pollution and eutrophication) (Table 1).

In the following, we will investigate the nature of lake responses according to the criteria used to classify three types of regime shifts described in Andersen et al. (2009) while also considering these different driver pathways. The conceptual framework provided by Andersen et al. (2009) may not recognize other possible types of regime shifts including those with slow, smooth variable rate transition (Seekell et al. 2013; Hughes et al. 2013). We focus our analysis on recent studies that infer ecosystem changes from sedimentary diatom assemblages. The 22 examples are summarized in Table 1. Of the 34 papers included in this review, only nine specifically use the term “regime shift”. The duration of the regime shift and identification of the main drivers are either described in the paper or estimated from the data presented in the individual studies.

Table 1 Summary of studies included in this paper sorted by main driver

No.	Main driver	Regime shift type	Time of shift (cal. yr b2 k)	Duration of shift (years)	Duration of driver change (years)	Main reference
1	Climate: ice cover	I	8250	c. 25	c. 25	Anderson et al. (2008)
2	Climate: ice cover	II	5850, 4150	300–400 ^a	3000–4000	Rouillard et al. (2012)
3	Climate: ice cover	II	1450	c. 200	c. 500	Mackay et al. (2012)
4	Climate: ice cover	II	150	c. 20–50	c. 200	Rühland et al. (2008), Smol et al. (2005)
5	Climate: precipitation	I	8090	5–10	c. 2–5	Randsalu-Wendrup et al. (2012)
6	Climate: precipitation	II	70	5	10–20	Stone and Fritz (2004)
7	Climate: precipitation	II	1050	30–50	200–300	Reuss et al. (2013)
8	Climate: mixing and stratification	II	7900	5–10	200–300	Randsalu-Wendrup et al. (2012)
9	Climate: mixing and stratification	II	850	20–30	c. 500	Bracht et al. (2008)
10	Climate: catchment vegetation	II	3050	100–200 ^a	300–500	Pienitz et al. (1999)
11	Climate: catchment vegetation	II	1800	c. 200	c. 1500	Reuss et al. (2010)
12	Lake ontogeny + ice cover etc.	II	6850	250	c. 2000 (alkalinity), c. 500 (climate)	Paul et al. (2010)
13	Lake ontogeny + precipitation, ice cover	II	1050	c. 200–300	c. 7000	McGowan et al. (2003)
14	Anthropogenic: deforestation	I	2480	c. 150 ^a	c. 150	Bradshaw et al. (2005)
15	Anthropogenic: pollution	III	35	c. 5	c. 5	Sayer et al. (2006)
16	Anthropogenic: eutrophication	III	35	10–20 ^a	100–200	Rasmussen and Anderson (2005)
17	Anthropogenic: eutrophication, lake level changes	III	50	1–4	c. 30	Hobbs et al. (2012)

Duration of regime shift and duration of driver change has been estimated from data presented in the individual studies

^a Temporal resolution of record constrains timing of regime shift

Type I: Smooth regime shift

Because of the often inherently slow forcing of climate (slow in comparison with the life cycles of organisms in limnological ecosystems), examples of smooth pressure regime shifts are not very abundant in the paleolimnological literature. The threshold is present in the forcing variable (Fig. 1a), and relatively few studies have examined how these climatic thresholds affect ecosystems. One issue in identifying an ecological response to a threshold in the driver is the potential for smoothing of the signal in the paleolimnological records and inherent uncertainties in

chronological control, although these problems are mitigated in sites with varved sediments and good chronologies. For example, in a varved lake in mid-central Sweden, an abrupt change in precipitation associated with the abrupt cooling of the 8.2-ka event in the North Atlantic-region led to increased erosion in the catchment, an abrupt increase in nutrients entering the lake, and a shift within the lake to higher primary production, with a doubling of diatom accumulation rates over a period of 5–10 years (Randsalu-Wendrup et al. 2012; Table 1, no. 5). Similarly, but on a different scale, a cold, dry event approximately 8200 years ago led to prolonged ice cover in a lake

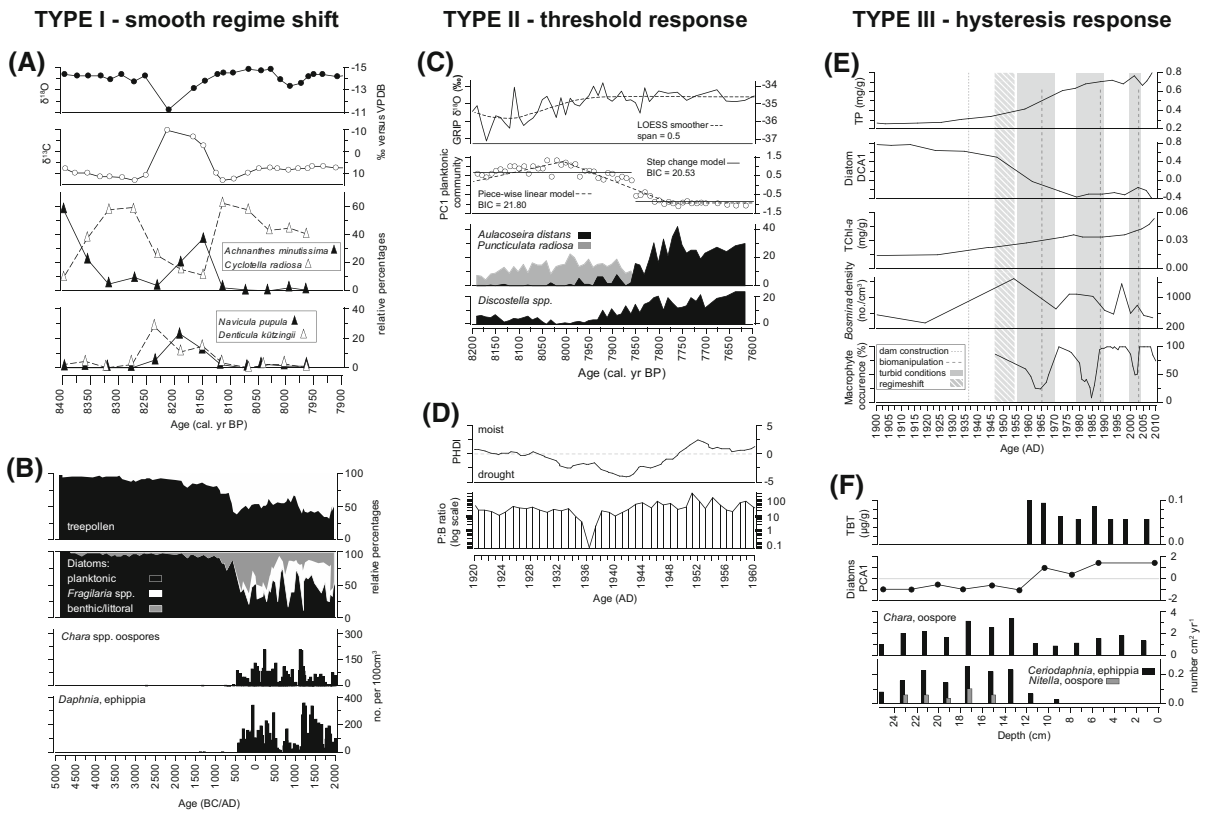


Fig. 2 Examples of different types of regime shifts from the literature. Type I, smooth regime shift: **a** profiles of key diatom species, $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ isotope records redrawn from Anderson et al. (2008). The increase in $\delta^{18}\text{O}$ indicates increased aridity, while the coincidental reduction in $\delta^{13}\text{C}$ reflects a reduction in productivity (Anderson et al. 2008). Simultaneous with the climate changes recorded by the isotope record is a significant decrease in planktonic *Cyclotella radiosa* (Grunow) Lemmermann 1900, and a corresponding increase in periphytic *Achnanthes minutissima* Kützing 1833, *Navicula pupula* Kützing 1844 and *Denticula kuetzingii* Grunow 1862, **b** summary proxy data describing the development of Dallund Sø and the landscape surrounding the lake redrawn from Bradshaw et al. (2005). At c. 500 BC there is an abrupt decrease in the amount of tree pollen, accompanied by decreased proportions of planktonic diatoms and the appearance and expansion of charophyte vegetation and pelagic *Daphnia* spp. Type II, threshold-like regime shift: **c** $\delta^{18}\text{O}$ record from the GRIP ice core, first principle component of the planktonic community and time series of key diatom species redrawn from Randsalu-Wendrup et al. (2012). PCA1 of the planktonic community was analysed for change-points over time using a combination of abrupt step

changes and piece-wise linear regressions (Randsalu-Wendrup et al. 2012). The optimal change-point model (assessed by the lowest BIC) is shown with solid lines, and the alternative less suitable model with dashed line. **d** 5-year running average of monthly regional moisture as measured by the Palmer hydrologic drought index (PHDI) and the annual record of planktic to benthic diatom ratio (log-scale) at Foy Lake. Redrawn from Stone and Fritz (2004). A pronounced increase in benthic diatoms occurred in the mid-1930s, simultaneous with a long period of regional drought. Type III, hysteresis-like regime shift: **e** Proxies of lake trophic status (TP), diatom assemblage turnover (Diatom DCA1), primary production (TChl-*a*) and *Bosmina* remains over the last 110 years, and submerged aquatic plant survey data since 1947 from Lake Christina. Redrawn from Hobbs et al. (2012). **f** TBT profile, first principle component of diatom community, fluxes of *Chara* and *Nitella* oospores and remains of zooplankton *Ceriodaphnia* from Hickling Broad, redrawn from Sayer et al. (2006). With the appearance of TBT in the lake, there is a loss of submerged vegetation and zooplankton as well as a shift in diatom community composition

in southwest Greenland (Anderson et al. 2008; Table 1, no. 1; Fig. 2a). A resulting reduction in lake turbulence and decreased catchment weathering and nutrient inputs led to a major reduction in lake

productivity and an abrupt shift from a planktonic to a periphytic algal community, similar to the pattern observed in many contemporary Arctic and high-altitude lakes (Lotter and Bigler 2000). The regime

shift took place over approximately 25 years, and the system remained in the cold state for 50 years before returning to its former state, at approximately the same rate as the climate change.

Rapid threshold-like changes in drivers are often anthropogenic in nature. In Danish lake Dallund Sø (synthesized in Bradshaw et al. 2005; Table 1, no. 14) major, rapid deforestation around 500 BC led to enhanced catchment erosion and increased nutrient input into the lake, as well as lake infilling and shallowing. The changes in water depth and in-lake nutrient concentration led to extreme changes in the aquatic environment: an expansion of submerged vegetation, higher in-lake productivity and associated changes in the diatom flora (Fig. 2b). The lake, which was originally an oligotrophic system, changed to a eutrophic system. The new regime appeared to be more sensitive to external forcing from the catchment based on a change in the diatom data from an early interval of relative stability to a subsequent period during the Iron Age (500 BC–AD 1050) of marked fluctuations in the ratio of planktonic/nonplanktonic diatoms, which continued to the modern day. This variability may, to some extent, also be a function of intensified anthropogenic impact over time.

Type II: Threshold response

In tipping-point regime shifts, 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; Fig. 1b). 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 can be quite heterogeneous, i.e. different lakes react differently to the same forcing (Williams et al. 2011).

Climate

Direct climate impacts on ice cover can cause regime shifts. Long periods of ice-cover, promoted by cool temperatures, can inhibit primary production and

habitat availability, whereas decreased ice cover duration may increase the length of growing season and the duration of water column stratification (Mackay et al. 2012; Catalan et al. 2013). Ice cover responds in a non-linear fashion to small changes in temperature (Weyhenmeyer et al. 2004), thus relatively subtle temperature changes can cause dramatic changes in lake state.

Rapid ecological reorganizations, which have been attributed to recent climate warming mediated through changing ice-cover dynamics, are presently occurring in lakes throughout the Northern Hemisphere (Smol et al. 2005; Smol and Douglas 2007; Rühland et al. 2008; Rouillard et al. 2012; Table 1, no. 4). Although these regime shifts are manifested at several trophic levels (Smol et al. 2005), the shifts have been described mainly from changes in the species composition of diatom communities and are characterized by increases in small planktonic diatoms, such as *Cyclotella* species, and a compensatory decrease in small periphytic (often *Fragilaria*) species. The changes suggest shorter periods of ice-cover, longer growing seasons and increased thermal stratification (Rühland et al. 2008). Rühland et al. (2008) reject nutrient dynamics as a contributing mechanism in the shifts, while Saros et al. (2012) argue that interplay between light, thermal stratification and nitrogen availability is driving the diatom changes. Nonetheless, given the inherently non-linear responses of ice cover to climate change (Weyhenmeyer et al. 2004), we consider it likely that these changes are threshold-like.

A similar ecological regime shift connected to climate warming, although earlier in time, has been described from an alpine lake in southern Siberia during the Medieval Climate Anomaly (Mackay et al. 2012; Table 1, no. 3). A major shift in diatom species composition at 1400 cal. yr BP is characterized by a marked decline in fragilarioid taxa, concomitant with an increase in species diversity as a result of greater habitat availability due to shorter ice-cover duration. An additional contributor to ecosystem change at this site is a lowering of lake water pH as a result of permafrost melting and increased DOC export from forest soils (Mackay et al. 2012).

Lakewater pH has been proposed as an important driver of diatom assemblage changes in poorly buffered Arctic and Alpine lakes, with warm intervals resulting in higher pH values due to enhanced loss of CO₂ to the atmosphere and greater utilization of

limnetic CO₂ by algal photosynthesis, compared with cooler periods with longer ice-cover (Michelutti et al. 2007; Rouillard et al. 2012; Wilson et al. 2012; Fritz and Anderson 2013). Two poorly buffered lakes in the high Arctic of Canada show regime shifts, with a shift in diatom dominance from small benthic *Fragilaria* taxa to a more diverse but less productive assemblage of small benthic and periphytic species, including slightly acidophilous *Achnanthes* and *Navicula* taxa (Rouillard et al. 2012; Table 1, no. 2). The dynamics behind the shifts are connected to the neoglacial cooling caused by decreasing summer insolation from the mid- to late Holocene, and the associated lengthening of ice cover and decreased lakewater pH (Rouillard et al. 2012). The shifts, however, occur with a lag of approximately 1200-years relative to the cooling trend as a result of carbonate-rich glacial tills that buffered the lakes. This emphasizes the importance of lake catchment characteristics in determining lake response to direct climate change.

In addition to influencing ice-cover, changes in temperature and associated changes in wind patterns can influence lake thermal stratification and mixing regimes directly (Panizzo et al. 2008; Medeiros et al. 2012). This, in turn, has a strong influence on the competitive abilities of phytoplankton either by directly controlling their buoyancy or indirectly controlling the availability of nutrients (Battarbee 2000). A regional change in climate in the Rocky Mountains at the onset of the Little Ice Age caused ecosystem changes in Crevice Lake, Montana, where changes in planktonic diatom species composition were driven by changes in the length and stability of summer stratification relative to the length of isothermy following ice melt (Bracht et al. 2008; Table 1, no. 9). At c. 800 cal. yr BP a large and abrupt increase in *Stephanodiscus* spp. occurred, likely caused by a transition to long, cool springs with extended periods of mixing. This occurred at the middle of the global cooling trend between the Medieval Climate Anomaly (1500–1000 cal. yr BP) and the Little Ice Age (500–100 cal. yr BP) (Marcott et al. 2013). Bracht-Flyr and Fritz (2012) compare diatom records from four lakes in western Montana (including Crevice Lake), which display different responses at roughly the same time (800–600 cal. yr BP), emphasizing the importance of local ecosystem characteristics in mediating climate impacts on biological communities. The pattern in Crevice Lake is similar to that observed

by Smol et al. (2005), Rühland et al. (2008) and others: a dominance of *Cyclotella* spp. associated with warmer conditions and enhanced stratification of the water column.

A similar diatom response occurred with the gradual climate warming after the cooling of the 8.2-ka event in mid-central Sweden (Randsalu-Wendrup et al. 2012; Table 1, no. 8; Fig. 2c). 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 (Randsalu-Wendrup et al. 2012).

Precipitation variability also influences lake ecosystems directly (Leavitt et al. 2009), and changes in the balance between precipitation and evaporation influence salinity and lake level, which, in turn, can drive regime shifts in lake ecosystems (Fritz et al. 2000; Laird et al. 2003). A regime shift from a dilute, oligotrophic lake to a lake with strong seasonal chemical stratification, hypolimnic anoxia and a large phototrophic bacterial production at c. 900 cal. yr BP was observed in Lake SS86 in western Greenland (Reuss et al. 2013; Table 1, no. 7). The regime shift was marked by a shift from algal pigments to near complete dominance of pigments specific to green sulphur bacteria, which require photic zone anoxia to grow. The shift occurred in the latter part of the Medieval Climate Anomaly, and the authors propose that reduced precipitation caused lake-level lowering. Due to its morphometry, when the lake level dropped below the outlet level, the lake became a closed basin. This allowed for a different set of feedback mechanisms to dominate the lake, and stratification rather than precipitation became the strongest influence on ecosystem state. The climate change during the Medieval Climate Anomaly was gradual, as likely was the lake level lowering, but as the lake reached a threshold (in this case a lowering beneath an actual, physical threshold) a rapid regime shift occurred.

Lake morphometry also plays a major role in controlling regime shifts in Foy Lake in the North American Rocky Mountains, where large and rapid spikes in benthic diatom abundance during the last 800 years were likely caused by relatively small changes in lake level that produced large changes in the amount of habitat available for benthic diatoms (Stone and Fritz 2004; Stevens et al. 2006; Table 1, no. 6). The Foy Lake record shows regime shifts that result

from an interaction of climate change and lake morphology, with climate causing lake level lowering through altered precipitation-evaporation balance, but morphology determining the diatom response to these (sometimes small) climatic shifts.

In forested catchments, or catchments close to the tree line, changes in vegetation affect the supply of DOC and nutrients to lakes, influencing aquatic communities and biological productivity (Anderson et al. 2008; Mackay et al. 2012). Direct influence of treeline dynamics on lake ecosystems is shown by Pienitz et al. (1999; Table 1, no. 10), who reconstructed an abrupt shift in diatom composition and a rapid decrease in lake-water DOC content following the retreat of spruce (*Picea abies* (L.) H. Karst.) from the catchment of a subarctic Canadian lake (Queen's Lake). The sensitivity of the lake was influenced by its dilute nature (Pienitz et al. 1999). Several other studies have shown abrupt changes in geochemical proxies in response to treeline retreat or advance, whereas biological proxies often show more diverse or delayed responses. Reuss et al. (2010; Table 1, no. 11) describe an abrupt ecological shift in a subarctic lake at tree-line in northern Sweden, at c. 1750 cal. yr BP, when a drop in the C/N ratio, significant changes in the chironomid communities and a shift in the phototrophic community from diatom dominance to increased influence of chlorophytes suggest expansion of aquatic mosses. This is connected to a period of continued late-Holocene cooling and is followed by a shift in diatom composition to benthic dominance around 1000 cal. yr BP. General treeline retreat in the area started around 3200 cal. yr BP, with resulting soil destabilization and increased wind exposure of the lake. The shift at 1750 cal. yr BP is likely a threshold response of the aquatic ecosystem to the treeline retreat, following a long period of gradual changes in physical and chemical properties of the lake that altered habitat availability. Other studies have also shown major limnological change associated with climate-driven impacts mediated through catchment and vegetation dynamics (Jones et al. 2011), but many show gradual changes rather than regime shifts.

Lake ontogeny

Lakes inherently change as they age and, as newly formed landscapes evolve, physical and biological changes occur that are collectively known as primary

succession. The ontogenetic processes may proceed in a non-linear manner (Engstrom et al. 2000), and the constantly shifting baselines mean that a similar external forcing may influence the same lake in a contrasting way depending on the stage of lake development. For example, Braya Sø, a closed-basin oligosaline lake in West Greenland, has displayed several abrupt shifts in lake salinity (as conductivity inferred from diatoms) and lake level (inferred from radiocarbon dating of lake terraces) throughout the Holocene (McGowan et al. 2003, Table 1, no. 13; Fritz 2008; Aebly and Fritz 2009). McGowan et al. (2008) showed that lake response changed as the lake aged; a slow accumulation of salts (increasing conductivity) through time eventually allowed a threshold to be crossed at c. 1000 years BP, and after this point the lake alternated between meromixis and fully mixed states. Meromixis involves the isolation of denser saline bottom waters from the upper fresher mixed layer, and the availability of salts is a necessary antecedent condition. Within the latest 1000 years of the Braya Sø record, the cessation of the meromictic state resulted in larger fluctuations in salinity than would occur in a dimictic or monomictic lake, because of the entrainment of the highly saline bottom layer into surface waters (McGowan et al. 2003). The resultant abrupt shifts in mixing status resulted in very different algal communities, with cyanobacteria dominating during mixed periods and purple sulphur bacteria during periods of meromixis (Anderson et al. 2004). Thus, in some lake states a relatively small change in the precipitation-evaporation balance can produce a disproportionate response in the physico-chemical properties of the lake, causing reorganization of the community structure and a regime shift.

Similarly, reconstructions from a small low Arctic lake 200 km north of the forest-tundra ecotone in mainland Nunavut, Canada (Paul et al. 2010; Table 1, no. 12) also demonstrate the importance of natural lake development and lake age in determining lake response to climate forcing. A rapid and almost complete diatom species turnover occurred around 6800 cal. yr BP in response to climate warming at the onset of the Holocene Thermal Maximum (Rühland 2001; Smol et al. 2005, Mackay et al. 2012), with an associated increase in the open-water period and longer growing seasons. However, the authors argue that the shift is also likely attributable to a natural

long-term loss of alkalinity in the lake because of a transition to a less alkaline diatom assemblage. Paul et al. (2010) argue that the abruptness of the shift suggests that the combination of long-term alkalinity loss, driven by the depletion of base cations from the developing soils and the increased contribution of organic acids from surrounding vegetation, together with factors mediated by warmer climate (i.e. shorter ice-cover duration, longer growing season) led to the crossing of a critical threshold and the observed regime shift.

Type III: Hysteresis response

In bistable systems with hysteresis, the trajectory of the response variable will be different for increasing versus decreasing modes of the driver (Andersen et al. 2009; Collie et al. 2004). A single transition from one state to another is the same for the non-linear threshold and the hysteresis responses (Fig. 1b, c). Demonstrating hysteresis requires data where the driver is both increasing and decreasing, giving rise to shifts between states occurring at different thresholds (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 et al. 2012), and in paleolimnological studies it is often difficult to evaluate whether different states exist under the same conditions (i.e. alternative stable states), partly because the non-stationary baseline associated with lake ontogeny, as described above, changes the driver-ecosystem response independent of the direction of change in the driver.

Bistable systems with hysteresis are often described as “alternative stable states” in the limnological literature, and shallow lakes are commonly used as examples, because they, if simplified, commonly alternate between two states: one characterized by dominance of aquatic plants and clear water and the other by phytoplankton dominance and turbid water (Scheffer et al. 1993). Often, however, changes between states may occur gradually or cyclically or evolve via a transition state (Hargeby et al. 2007; Scheffer and van Nes 2007; Sayer et al. 2010b).

Shallow lakes as bistable systems with hysteresis are especially well studied in association with anthropogenic eutrophication (Jeppesen et al. 1998;

McGowan et al. 2005; Scheffer and van Nes 2007; Scheffer and Jeppesen 2007; Hargeby et al. 2007; Zimmer et al. 2009, Sayer et al. 2010b). Regime shifts are often the result of multiple stressors, and, in many cases, the changes in forcing variable have exposed the ecosystems to conditions beyond the range of natural variability (Collie et al. 2004). Lake Christina in Minnesota, USA, showed a dramatic regime shift in c. 1950 from a stable clear-water, macrophyte-dominated state to a managed period with turbid phytoplankton-dominated states (Hobbs et al. 2012; Theissen et al. 2012; Table 1, no. 17; Fig. 2e). The regime shift was a consequence of multiple stressors working over an approximately 30 year period: eutrophication beginning in the 1930s and 1940s that made the lake more unstable and susceptible to a regime shift and increased annual rainfall which, along with the construction of a dam on the main outlet of the lake, increased water levels (Hobbs et al. 2012). After the shift into turbid conditions, the lake has been managed through fish removal three times (1965, 1987 and 2003). These manipulations have increased water clarity and the extent of submerged aquatic plants, but the improvements were temporary and persisted only approximately 10 years following 1965 and 1987 and five years after 2003. The biomanipulation seemed to move the ecosystem back and forth along a turbidity gradient, but ultimately a return to a clear-water ecosystem is not possible without the reduction of nutrients to limit algal production (Hobbs et al. 2012); thus the lake shows hysteresis-like behavior. The variable stability of alternative states was also evident in the shallow Danish Gundsømagle Sø, which, after a smooth regime shift around 1300 BC was mesoeutrophic, with an extensive and diverse aquatic flora for more than 3000 years, despite extensive agriculture and climate variability (Rasmussen and Anderson 2005; Table 1, no. 16). Around 1960, however, the submerged vegetation collapsed, and floating-leaved *Nymphaeaceae* vegetation expanded, probably as a result of sustained anthropogenic stress with unprecedented levels of erosional input and external nutrient loading (Rasmussen and Anderson 2005).

Other anthropogenic stressors can also perturb lake ecosystems and cause changes in concert with eutrophication: one example is from the Norfolk Broads, UK, where the introduction of toxic tributyl tin (TBT) as an antifouling paint on boats in the lakes in the 1960s caused regime shifts, with a dramatic loss

of submerged vegetation, the replacement of macrophytes by phytoplankton and a shift in associated diverse animal communities (Sayer et al. 2006; Table 1, no. 15; Fig. 2f). The resilience of the system was already low due to eutrophication, fish kills and increased salinity, but the proximate driver of the shift was a reduction in grazing invertebrates, particularly molluscs and zooplankton, by TBT (to which it is highly toxic). The breakdown of a feedback loop that had reinforced plant dominance led to dense growths of periphytic and planktonic algae and a rapid loss of aquatic vegetation (Sayer et al. 2006).

As stated earlier and illustrated in the examples above, most of these types of regime shifts are studied in shallow lake systems affected by anthropogenic impact (mainly eutrophication). The role of climate in triggering switches between alternative states is controversial (Jeppesen et al. 2003), but it has been suggested that changes in temperature can alter water clarity by influencing zooplankton grazing potential (Scheffer et al. 2001a; Jeppesen et al. 2003) and that physical disturbance from hurricanes (Bachmann et al. 1999; Lowe et al. 2001) or water level change (Blindow 1992; Blindow et al. 1993) can initiate state changes.

Perspectives

It is well established that regime shifts in lake ecosystems can occur as a result of both abrupt and continuous climate change, and that regime shifts may leave an imprint in paleolimnological records, allowing us to investigate and better understand patterns and processes governing abrupt ecological changes on a geological timescale. In our literature survey we examined the relations between the duration of change in driver and the duration of the regime shift (Fig. 3). In keeping with our conceptual model (Fig. 1), 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. The exception is Sayer et al.'s (2006; Table 1, no. 15) study of regime shifts caused by TBT, classified as type III but displaying type I-like behaviour with the regime shift from clear water to turbid conditions occurring as an immediate response to the change in driver (introduction of TBT). This

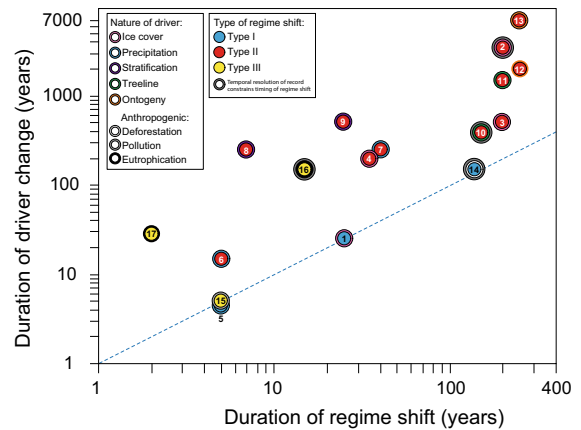


Fig. 3 Duration of regime shift plotted against duration of driver change. Numbers refer to reference numbers in Table 1. Dashed blue line is a 1:1 line showing regime shift duration equalling duration of driver change

discrepancy highlights the importance of driver selection when classifying regime shifts: because the multitude of drivers affecting lake ecosystems act on different timescales, the classification of ecosystem response to a changing driver depends on which driver is the focus of the investigation. The ecosystem described in Sayer et al. (2006) is 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 becomes the proverbial straw breaking the camel's back, forcing the system into a turbid state, which is then maintained even when TBT inputs are reduced. Thus characterizing this transition as a type III regime shift is appropriate. Similarly, a focus on precipitation as the main driver of the regime shift described in Reuss et al. (2013) led to its classification as type II, but had we instead focused on lake characteristics (open or closed lake basin), the regime shift would be classified as type I, with a threshold crossed in the driver (basin becoming closed), which gave rise to an abrupt ecosystem change. In general, climate-related drivers and physical processes act on similar timescales, and we demonstrate that these drivers can give rise to regime shifts that can be classified as either smooth, threshold-like or bistable.

A common problem in working with paleolimnological records in general, and when investigating regime shifts in particular, is low temporal resolution. In some of the literature used in our analysis (Fig. 3),

the temporal resolution of the record limits identification of the timing and rate of the regime shifts. In these examples, 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 1 year. However, in all of the examples the forcing is acting on even longer time scales (Table 1; Fig. 3), allowing identification of the general dynamics driving the shift, although the specifics are hidden in the time integration inherent in sediment records. Resolution is also an important factor when discussing terminology and definitions: a shift in ecosystem state is generally considered a regime shift if it is abrupt and persistent (Folke et al. 2004; Lees et al. 2006; Andersen et al. 2009; Williams et al. 2011). But what is persistent on a geological time scale? Anderson et al. (2008) describe a regime shift where the system stays in the new regime for 50 years before shifting 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 here, the shift might not be evident in the record due to low time resolution.

It is difficult to extrapolate ecosystem responses over space and time, because ecosystem responses to the same forcing mechanisms will differ among different systems and also change over time within the same system. In addition, the paleoclimate history at any one site is always imperfectly known, making it difficult to rule out the possibility that abrupt ecological changes observed at one site were in fact forced by an unknown but suddenly changing external driver (Williams et al. 2011). Using multiple records from the same region, however, can help overcome this problem. Bracht-Flyer and Fritz (2012) showed that at a regional scale external climate events can simultaneously force multiple local systems into new states, although the rate and characteristics of the changes vary among sites. Similarly, Smol et al. (2005), Rühland et al. (2008) and others showed the same patterns of change in response to climate warming across the northern hemisphere, although individual lakes responded in a site-specific manner. Thus, independent evidence of the nature of the forcing mechanism can be derived by regional replication from multiple sites, or indeed from other proxies at the same site.

One of the remaining challenges in understanding regime shifts and ecosystem dynamics in a

paleolimnological perspective is that we lack the tools to thoroughly identify system feedback mechanisms. Sayer et al. (2010a), Battarbee and Bennion (2012) and Battarbee et al. (2012) argue that the solution to this is to combine contemporary ecology and paleolimnology. Linking the timescales of these approaches can allow us to disentangle the role of different forcings on lake ecosystems and to understand the mechanisms behind ecosystem responses to these forcings. The strength of paleolimnology in this setting is perhaps not only to look directly at individual changes, but to be able to use long sediment records to really understand the mean state of a lake ecosystem, identify natural variability of states and the degree of their persistence in relation to lake history, and to identify real departures from the mean state. 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.

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