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A 200-year perspective on alternative stable state theory and lake management from a biomanipulated shallow lake

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Abstract. Multiple stressors to a shallow lake ecosystem have the ability to control the relative stability of alternative states (clear, macrophyte-dominated or turbid, algal-dominated). As a consequence, the use of remedial biomanipulations to induce trophic cascades and shift a turbid lake to a clear state is often only a temporary solution. Here we show the instability of short-term manipulations in the shallow Lake Christina (Minnesota, USA) is governed by the long-term state following a regime shift in the lake. During the modern, managed period of the lake, three top-down manipulations (fish kills) were undertaken inducing temporary (5–10 years) unstable clear-water states. Paleoecological remains of diatoms, along with proxies of primary production (total chlorophyll *a* and total organic carbon accumulation rate) and trophic state (total P) from sediment records clearly show a single regime shift in the lake during the early 1950s; following this shift, the functioning of the lake ecosystem is dominated by a persistent turbid state. We find that multiple stressors contributed to the regime shift. First, the lake began to eutrophy (from agricultural land use and/or increased waterfowl populations), leading to a dramatic increase in primary production. Soon after, the construction of a dam in 1936 effectively doubled the depth of the lake, compounded by increases in regional humidity; this resulted in an increase in planktivorous and benthivorous fish reducing phytoplankton grazers. These factors further conspired to increase the stability of a turbid regime during the modern managed period, such that switches to a clear-water state were inherently unstable and the lake consistently returned to a turbid state. We conclude that while top-down manipulations have had measurable impacts on the lake state, they have not been effective in providing a return to an ecosystem similar to the stable historical period. Our work offers an example of a well-studied ecosystem forced by multiple stressors into a new long-term managed period, where manipulated clear-water states are temporary, managed features.

Key words: algae; alternative stable state; biomanipulation; Bosmina; *diatoms; Lake Christina; lake sediments; macrophytes; paleolimnology; regime shift; shallow lake; waterfowl.*

Introduction

The deterioration of shallow lakes from a clear-water, macrophyte-dominated state to a turbid, phytoplankton state has been observed and described theoretically through the concept of alternative stable states (Fig. 1) (Scheffer et al. 1993, Scheffer and Carpenter 2003). The relative stability of turbid and clear-water states as determined by external conditions (e.g., nutrients) can be such that long-term establishment of a stable clear, macrophyte state is not possible once the ecosystem has been significantly perturbed unless the external conditions are dramatically reduced (Fig. 1a). In this context we refer to this perturbation as a "regime shift," in other words a change in the ecosystem between *stable* clear and turbid states (Scheffer and Carpenter 2003).

Ecosystem-scale biomanipulations have been used to demonstrate threshold responses in shallow lakes (Hanson and Butler 1994*a*, *b*, Jeppesen et al. 1997, Scheffer 1998). Often they are implemented as remedial approaches to improve water quality impaired by a dominance of phytoplankton, high turbidity, and high nutrient levels. In a number of cases the introduction of piscivorous fish and/or the removal of planktivores have induced trophic cascades, indirectly affecting changes in primary production (Hanson and Butler 1994*a*, Carpenter et al. 2011). Remediation efforts through

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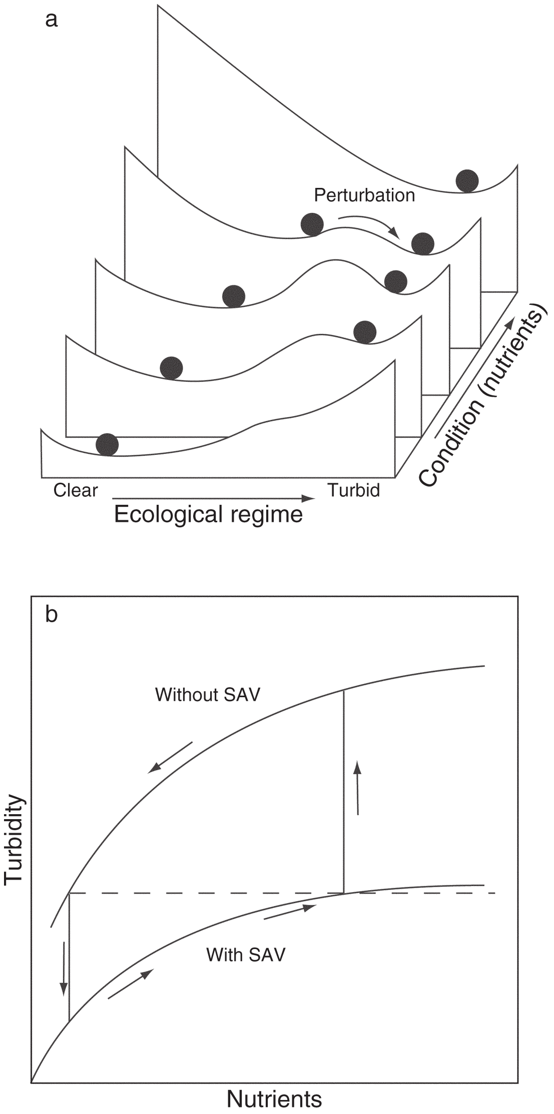

FIG. 1. Theoretical predictions for nutrient-driven shifts across alternative states in shallow lakes. (a) Theory predicts that the stability of the clear-water state declines as nutrients increase, with a corresponding increase in the stability of a turbid state. Perturbations can cause a regime shift in the lake at moderate levels of nutrients, but the only possible states at low and high nutrient concentrations are clear and turbid, respectively. (b) Alternative stable states (turbidity) in shallow lakes as a function of nutrient levels, showing the possible hysteresis present following a reduction in external nutrient loading. The dashed line represents the critical turbidity boundary. This model assumes a dependent relationship among nutrients, turbidity, and submerged aquatic vegetation (SAV). The figure is modified from Scheffer et al. (1993) and Scheffer and Carpenter (2003).

biomanipulations on shallow, turbid lakes can be hindered by the hysteresis of internal nutrient loading (Fig. 1b; see also Jeppesen et al. 2005). Thus, it has been suggested that a dramatic reduction of external and/or internal nutrient loading is necessary in concert with top-down manipulations to sustain a clear stable state once the system has been perturbed (McQueen 1998, Benndorf et al. 2002, Jeppesen et al. 2007).

Studies integrating both contemporary and paleolimnological data on shallow lakes have successfully described the historical context for modern deterioration of macrophyte communities and water quality (Davidson et al. 2005, Sayer et al. 2010), but few, if any, have documented lake histories over periods of biomanipulation. Here we pair contemporary and paleolimnological approaches to differentiate between true regime shifts and unstable, short-term changes in lake state due to ecosystem biomanipulations.

Lake Christina is a large, shallow lake in the Upper Midwest United States and was once one of the most important feeding and staging areas for migratory waterfowl in the Mississippi Flyway. From 1900 to the mid-20th century the lake was particularly important for Canvasback Ducks (*Aythya valisineria*) (Smith 1946, Ordal 1966). Today the lake is a managed ecosystem and has been since its deterioration to a turbid phytoplankton-dominated state in the mid-1950s, which resulted in the loss of submerged aquatic vegetation and migratory waterfowl that rely on the plants. There have been three top-down biomanipulations using fish toxicants (1965, 1987, and 2003), while the lake was in a turbid state, to induce a fish kill and subsequent trophic cascades. Following the biomanipulations, each resulting clear state has been temporary, lasting from 5 to 10 years before deterioration of the water quality and loss of macrophytes. Many questions remain as to the driver of the lake's initial regime shift and why continued efforts to reverse it have failed. The objectives of this study were to (1) determine whether Lake Christina experienced turbid states prior to human settlement, (2) elucidate the drivers of the regime shift in the 1950s, and (3) establish whether alternative state changes induced by biomanipulations represent regime shifts or are temporary unstable features. Our compilation of multiple contemporary and paleoecological parameters documents how the effectiveness of short-term manipulations is ultimately governed by the long-term trophic status and stability of the lake and surrounding landscape.

METHODS

Study site

Lake Christina is an alkaline and eutrophic lake situated in the Prairie Pothole Region of Minnesota (46.0984° N, 95.7429° W; Fig. 2). The lake has a depth of 1.2 m over ~80% of the basin (total area of 1600 ha), with a small, deeper (4.3 m maximum depth), isolated basin on the eastern end (Fig. 2). The lake is situated in the Pomme de Terre River basin, on gray calcareous glacial drift deposits associated with the Alexandria stagnant moraine. The hummocky terrain surrounding the lake is typical of the kettle and knob or prairie pothole landscape of Wisconsin glaciation. The lake catchment is relatively small, there are no major fluvial inputs to the lake, and while groundwater is an important component of the drainage area, its relative influence on the hydrology is unknown. The main outlet from the lake is into Pelican Lake to the southwest. The late 1930s and early 1940s have been described as the best years for migratory waterfowl on Lake Christina, mainly Canvasback Ducks (Ordal 1966), possibly owing to the lack of suitable habitat in the region following the 1930s drought. Prior to 1900, the lake was used mainly by Lesser Scaup (*Aythya affinis*) and Redhead Ducks (*Aythya americana*).

History of damming and biomanipulations

Lake Christina has long been a focus of management, initially to address issues of water quantity and later to improve water quality related to migrating diving duck habitat. To conserve water during times of drought (e.g., 1930s), a dam was constructed at the outflow of Lake Christina in 1936. While mean water depths were greater following dam construction, the aerial extent of the lake did not increase. Starting in the 1950s, recurrent high turbidity, loss of submerged vascular plants, and declining fall use by diving ducks, led managers to treat the lake with fish toxicants three times; first during November 1965, then again in October 1987 and October 2003. The main targets of the treatments were the planktivores (bluegill *Lepomis macrochirus*, small yellow perch *Perca flavescens*, and big-mouth buffalo *Ictiobus cyprinellus*) and benthivores (bullhead *Ameirus* spp.) (see Hanson and Butler [1994*a*] for a description of the fish community response to the 1987 treatment). In general, water clarity, extent of submerged aquatic plants, and fall duck use increased following all three fish removals. However, the improvements from each biomanipulation were temporary and the effects persisted approximately 10 years following fish kills in 1965 and 1987, and only about 5 years after the 2003 treatment. Varying conditions after the treatments more than likely influenced the efficacy of these measures. For example, the 1965 treatment was followed by severe winter conditions and under-ice hypoxia, and the combined effects reduced the fish populations dramatically (T. Carlson, *unpublished data*). The persistence of the clear state following the 1987 manipulation compared with the short-lived clear state following the 2003 manipulation is due to several factors, including (1) 1987 was a thorough fish kill effectively extirpating most of the planktivorous fish; (2) following 1987, piscivores (largemouth bass *Micropterus salmoides* and walleye *Sander vitreus*) were stocked to control the planktivores; and (3) the deeper eastern basin of Lake Christina was aerated to provide an overwinter refuge for the piscivores (Hanson and Butler 1994*a*).

Modern limnological sampling

Limnological monitoring of Lake Christina began in 1985 and methods have remained consistent to present day (Hanson and Butler 1990, 1994*a*, *b*). Sampling has taken place at up to seven locations and at a minimum of five within the shallow western basin of the lake (Fig. 2). Epilimnetic water samples were collected during the open-water growing season (approximately late April through October) at a frequency ranging from every other week to once a month and analyzed for nutrients (total P, orthophosphate, total N, and dissolved inorganic N), total suspended solids, and chlorophyll *a* at the Minnesota Department of Agriculture Laboratory (Hanson and Butler 1994*a*, *b*; Table 1). At the time of

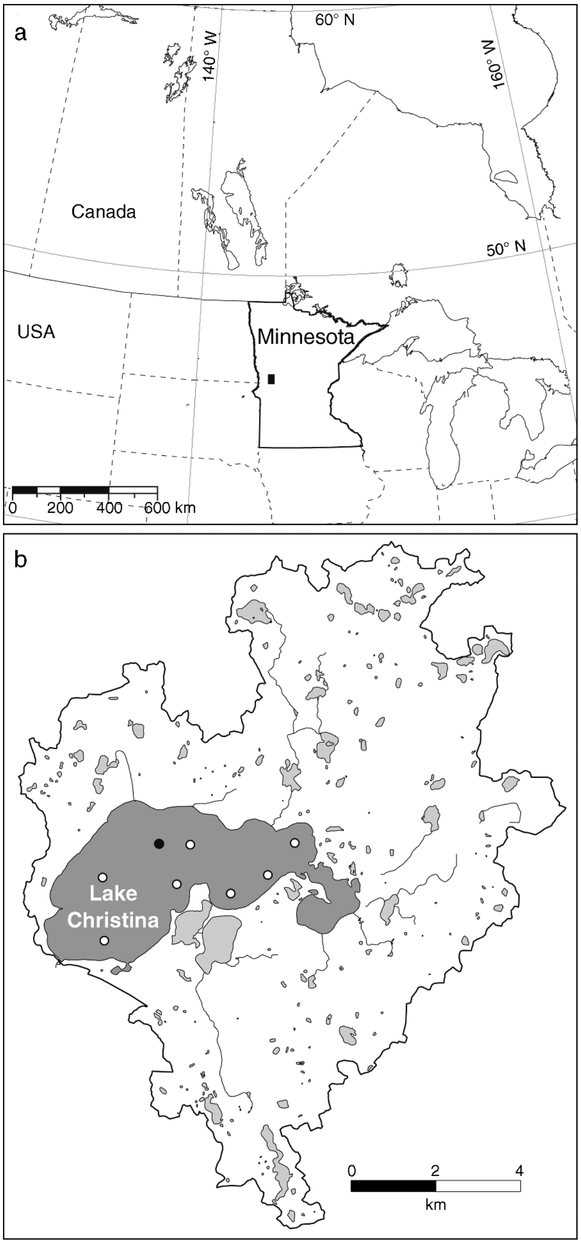

FIG. 2. (a) Site location map within Minnesota and (b) a detailed map of the hydrologic catchment. The black dot shows the sediment coring location, and white dots are the locations of water sampling.

TABLE 1. Mean summer epilimnetic data for Lake Christina.

Year	State	Water level† (m asl)	SAV‡ (%)	Secchi depth (m)	TSS (mg/L)	1% PAR depth§ (m)	20% PAR depth§ (m)
1985	turbid	369.84	8	0.3	70.73 (25.07)	0.54	0.38
1986	turbid	370.03	31	0.39	25.89 (22.03)	0.99	0.69
1987	turbid	369.72	57	0.46	38.82 (23.40)	0.97	0.68
1988	t-clear	369.60	95	0.53	33.37 (16.18)	1.04	0.73
1989	t-clear	369.73	97	0.68	23.4 (13.42)	1.32#	0.92
1990	clear	369.76	97	1.20#	4.25 (1.63)	2.37#	1.65#
1991	clear	369.84	100	1.20#	5.26 (5.03)	1.97#	1.38#
1992	clear	369.56	100	1.08	4.77 (3.12)	1.96#	1.37#
1993	clear	370.04	97	1.20#	3.97 (2.54)	2.31#	1.62#
1994	clear	369.74	100	0.92	7.88 (4.95)	1.48#	1.03
1995	clear	369.73	94	0.81	8.98 (4.22)	1.89#	1.32#
1996	clear	369.71	100	0.96	4.91 (2.70)	1.55#	1.08
1997	clear	369.68	100	1.08	4.07 (3.62)	1.84#	1.29#
1998	c-turbid	369.68	100	0.84	11.32 (4.50)	1.30#	0.91
1999	c-turbid	369.81	94	0.7	24.15 (12.76)	1.23#	0.86
2000	turbid	369.64	86	0.29	71.25 (23.81)	0.63	0.44
2001	turbid	369.99	66	0.37	58.6 (14.75)	0.91	0.64
2002	turbid	369.83	49	0.33	53.62 (12.32)	0.58	0.40
2003	turbid	369.62	51	0.33	56.89 (15.43)	0.76	0.53
2004	t-clear	369.79	100	0.49	28.69 (12.59)	1.21#	0.85
2005	clear	369.80	100	1.13	7.67 (8.90)	0.87	0.61
2006	clear	369.89	100	1.14	2.46 (1.22)	nm	nm
2007	clear	369.82	100	1.23#	6.34 (3.16)	nm	nm
2008	clear	369.74	100	0.79	16.29 (10.26)	nm	nm
2009	c-turbid	369.68	86	0.51	29.96 (11.89)	nm	nm

Notes: Number of samples range from 20 to 56 per open water season (April through October) collected over five monitoring stations. Standard deviations are in parentheses. The states t-clear and c-turbid represent the transition from turbid to clear and clear to turbid, respectively. Abbreviations are: asl, above sea level; TSS, total suspended solids; TP, total phosphorus; TN, total nitrogen; nm, light attenuation not measured; Unk, unknown.

† Water level measured at staff gauge in lake outlet.

‡ Submerged aquatic vegetation (SAV) coverage.

§ Calculated potential depth of attenuation of photosynthetically active radiation (PAR).

¶ Total peak waterfowl determined following methods of Howe and Carlson (1969).

\# Lake bottom.

water sampling, measurements were taken for water clarity (Secchi depth) and light attenuation (Table 1). Submerged aquatic vegetation (SAV) has been sampled since 1947, with annual sampling from 1980 to present (Fig. 3). Abundance estimates from weighted plant rake tows were compiled over at least 35 stations throughout the lake (Hansel-Welch et al. 2003).

Samples of phytoplankton and SAV (*Myriophyllum sibiricum* and *Stuckenia pectinata*) were also collected for analysis of stable isotope ratios and elemental abundance of C and N in the summer of 2006. SAV samples were frozen and immediately transferred to the laboratory for analysis. In the laboratory, samples were separated by species, scrubbed, washed with dilute acid to remove any precipitated inorganic C, dried and ground. Phytoplankton samples were collected by filtering lake water through 80 μm filters to remove zooplankton then filtering onto 0.7-μm precombusted Whatman glass fiber filters. Filters were dried and stored desiccated until time of analysis.

Sediment core collection and dating

Two sediment cores that were 0.75 m (CRWA09) and 0.83 m (CRWB09) in length were collected approximately 1.5 m apart, using a piston-type corer (Wright 1991) on 22 October 2009 at a water depth of 1.3 m (Fig. 2). Both cores were subsampled at a resolution of 0.25 cm; core CRWB09 was freeze-dried and prepared for diatom and all geochemical analyses, while core CRWA09 was left wet for analysis of zooplankton remains.

Geochronology was established on CRWB09 through ^{210}Pb decay (measured as ^{210}Po) by alpha spectroscopy and ^{137}Cs decay by gamma spectroscopy (Appleby 2010). The constant rate of supply (CRS) model was used to estimate ages and sediment accumulation rate (SAR) based on the radioactive decay of excess (or unsupported) ^{210}Pb above the background (or supported) ^{210}Pb activity (Appleby and Oldfield 1978). Confirmation of the 1963 Partial Test Ban Treaty ^{137}Cs peak was sought to confirm the ^{210}Pb age–depth model.

Diatoms and cladoceran remains

Sediments were processed for diatom sub-fossils using standard techniques for the oxidation of both carbonate minerals and organic matter and permanently mounted on slides for diatom enumeration (Battarbee et al. 2001). Diatoms were enumerated under oil immersion (numerical aperture = 1.4) at a magnification of 1000× using differential interference contrast optics. Several diatom floras were consulted for species identification (Kram-

TABLE 1. Extended.

Chl *a* (μg/L)	TP (mg/L)	TN (mg/L)	TN:TP (atomic)	Peak fall duck counts	Total peak waterfowl¶ (no. birds)
51.59 (29.63)	0.13 (0.04)	3.07 (0.62)	53.6	Unk	2 200
22.05 (10.79)	0.06 (0.02)	2.53 (1.12)	94.6	Unk	3 000
36.8 (21.25)	0.07 (0.02)	1.41 (0.40)	44.6	Unk	15 775
24.7 (13.57)	0.08 (0.03)	1.66 (0.63)	45.2	29 650	57 000
21.7 (15.34)	0.08 (0.02)	1.73 (0.60)	50.6	25 825	68 275
5.98 (8.18)	0.03 (0.01)	1.09 (0.16)	94.3	41 450	71 025
6.16 (4.13)	0.03 (0.02)	0.96 (0.25)	73.5	36 445	101 895
4.36 (1.87)	0.04 (0.01)	1.09 (0.19)	62.0	48 330	79 865
5.28 (3.74)	0.03 (0.01)	1.01 (0.21)	85.0	131 500	266 625
11.34 (6.95)	0.04 (0.01)	1.11 (0.22)	64.4	209 200	600 940
12.29 (5.61)	0.05 (0.02)	1.22 (0.22)	54.4	12 190	209 560
7.32 (4.40)	0.04 (0.01)	1.03 (0.22)	51.1	25 522	85 632
7.93 (5.61)	0.02 (0.02)	1.2 (0.25)	110.1	12 268	465 669
16.63 (6.44)	0.06 (0.02)	1.8 (0.48)	68.0	14 533	295 978
30.47 (14.05)	0.08 (0.03)	2.13 (0.66)	59.1	9 465	150 915
60.17 (18.51)	0.13 (0.02)	3.39 (1.04)	55.6	15 030	19 000
53 (15.74)	0.1 (0.02)	2.53 (0.34)	53.5	5 440	6 265
42.67 (13.51)	0.08 (0.02)	2.4 (0.41)	63.4	1 505	6 226
38.18 (8.23)	0.09 (0.02)	2.73 (0.67)	69.4	3 124	4 601
22.69 (8.87)	0.06 (0.02)	1.99 (0.29)	76.1	11 075	182 126
8.71 (5.58)	0.04 (0.02)	1.07 (0.21)	64.8	11 212	225 825
7.64 (3.93)	0.04 (0.01)	1.01 (0.22)	63.3	16 400	256 328
14.6 (5.79)	0.05 (0.01)	1.42 (0.47)	68.1	24 824	262 877
19.97 (11.00)	0.06 (0.02)	1.8 (0.38)	64.9	3 170	Unk
30.51 (10.51)	0.07 (0.01)	1.79 (0.45)	60.0	2 200	Unk

mer and Lange-Bertalot 1986, 1988, 1991*a*, *b*, Fallu et al. 2000) and photomicrographic documentation was conducted throughout the study using light microscopy. No evidence of frustule dissolution was noted during the analysis.

Sample processing for cladoceran remains was modified from Frey (1986) and Deevey (1942). Two to three grams of wet sediment were gently stirred in 150 mL of 10% KOH just below the boiling point for one hour. To preserve the smallest remains, samples were not rinsed through a screen but centrifuged and the supernate removed. Samples were brought back up to 50 mL with distilled water, shaken, and re-centrifuged. This process was repeated until the pH matched the value of distilled water in the lab. Processed samples were reconstituted in a Falcon tube with deionized water up to 20 mL. Two 1-mL subsamples were taken with a Hempsten-Stempel pipette and counted on a Sedgewick-Rafter cell at 100× with an Olympus BX50F4 microscope (Olympus Optical Company, Tokyo, Japan) capable of examination up to 400× for taxonomic purposes. Semi-permanent slide mounts in polyvinylpyrrolidone (PVP) were used for taxonomic verification. Results were converted to abundance (individuals/g dry sediment). Standard keys and monographs were used for taxonomic identification (Frey 1958, 1986, Balcer et al. 1984, Hann 1990, De Melo and Hebert 1994, Smith 2001, Sweetman and Smol 2006, Thorp and Covich 2009).

Sediment geochemistry

The physical composition of the sediments was established using loss-on-ignition (Heiri et al. 2001). Percent organic matter (% OM) was attained by combustion at 550°C, percent carbonate-C (% CO_3) at 1000°C, with remaining mass representing the non-carbonate inorganic fraction. Samples of sediment organic matter were analyzed for percent abundance of C and N and carbon stable isotopes ($\delta^{13}C$) following acid digestion to remove inorganic C (Verardo et al. 1990). All samples were analyzed by pyrolysis on a Carlo Erba NA1500 elemental analyzer/Conflo II device (CE Elantech, Lakewood, New Jersey, USA) coupled with a Finnigan Delta Plus mass spectrometer (Finnigan MAT, Bremen, Germany) in the Stable Isotope Laboratory at Stanford University. Organic C:N (atomic) values were calculated based on total organic carbon (TOC) and total nitrogen (TN) results. All $\delta^{13}C$ values are expressed relative to the Pee Dee Belemnite (PDB) standard. Approximately 5% of the samples were replicated yielding average standard deviations of 0.480% for TOC, 0.113% for TN, and 0.119‰ for $\delta^{13}C$.

We used a modified version of the method by Hieltjes and Lijklema (1980) for TP of freeze dried sediments. Briefly, TP was extracted using 30% H_2O_2 followed by 10 mol/L HCl in a shaking hot water bath and aliquots of the extracts were stabilized using 1 mol/L $Na_2S_2O_5$. Aliquots are then analyzed using the ascorbic acid method (Clescerl et al. 1999) with a flow-injection analysis auto-analyzer (Lachat Quikchem 8000; Lachat Instruments, Loveland, Colorado, USA). The percent relative standard deviation among method triplicate samples, which were run on 10% of the sediment intervals, was <2.5% (0.03 mg/g).

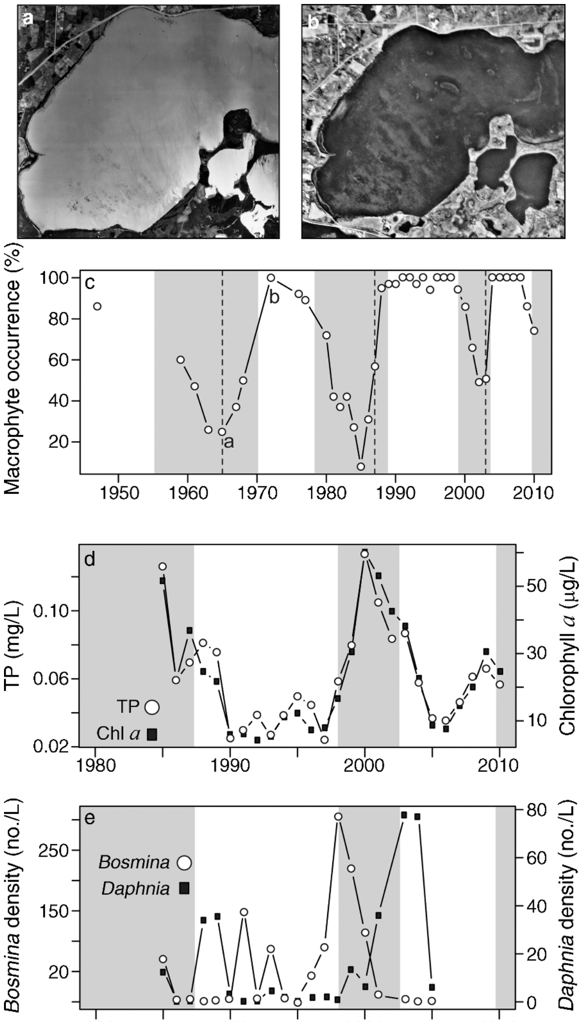

FIG. 3. Aerial photographs of Lake Christina in the (a) turbid state (4 August 1965) and (b) clear state (4 October 1972). (c) Submerged aquatic plant survey data compiled over 35 stations since 1947 with the aerial photograph dates marked for reference. (d) Mean total phosphorus (TP) and chlorophyll *a* (chl *a*) concentrations in water from five sampling stations collected during the open water season. (e) Mean *Daphnia* spp. and *Bosmina* spp. densities collected during the open water season. Shaded areas represent periods when the lake is in a turbid state. Photos provided by the John R. Borchert Map Library, University of Minnesota, Minneapolis, Minnesota.

Sediment proxies of lake primary production

Spectrally inferred total chlorophyll *a* (TChla) in sediments is a measure of both primary and derivative chlorophyll *a* compounds (i.e., primary chlorophyll *a* plus all chlorophyll *a* isomers, pheophytin *a*, and pheophorbide *a*) and has previously been shown to accurately assess the changing trophic status of lakes over time (Michelutti et al. 2010). Sediment preparation followed the methods outlined in Wolfe et al. (2006), and TChla determinations were calculated using the equation given in Michelutti et al. (2010). Briefly, sediments were first freeze dried and sieved (125 µm mesh size) to remove any possible confounding effects from differences in water content and grain size. Spectral measurements were performed with a Model 6500 series Rapid Content Analyzer (FOSS NIRSystems, Laurel, Maryland, USA) operating over the range of 400–2500 nm. Sediments were analyzed through the base of glass vials, with each sample representing an average of 32 scans. A ceramic reference paddle equipped in the Rapid Content Analyzer was used as a stable, consistent reflectance reference that was taken between every sample.

The total organic carbon mass accumulation rate (TOC MAR) can reflect the primary production of a lake if the organic C can be attributed to autochthonous processes. We calculated the TOC MAR using [TOC] (mg/g) multiplied by the sediment accumulation rate ($g \cdot m^{-2} \cdot yr^{-1}$) for each sediment interval.

Numerical analysis

Detrended correspondence analysis (DCA) was used to summarize the dominant gradient (i.e., DCA axis 1) of diatom compositional turnover (Hill and Gauch 1980). All diatom species were included in the analysis, detrending was by segments with downweighting of rare taxa, and nonlinear rescaling was applied. When plotted stratigraphically the DCA axis 1 scores show the amount of turnover between samples over time in units of standard deviation (SD).

A stratigraphically constrained cluster analysis was used to determine zones within the diatom stratigraphy based on Bray-Curtis dissimilarity distances (Grimm 1987). The zones were based on a uniform total sum-of-squares height and statistical significance was tested against a random broken-stick model (Bennett 1996). Multiple linear regressions and Pearson's product moment correlation coefficients were calculated for select untransformed variables. All statistical analyses were carried out using R (R Core Development Team 2011).

RESULTS

Modern limnology

Sampling of macrophyte occurrence since 1947 provides us with the distinct periods when Lake Christina was either turbid or clear (Fig. 3). The general trend of plant succession following manipulations from turbid to clear has been described in Hansel-Welch et al. (2003), where a pioneering plant community of *Najas flexilis*, *N. marina*, *Myriophyllum sibiricum*, and *Ruppia maritima* was found to establish the year after the manipulation, followed by a community of *Chara vulgaris*, *C. canescens*, *Stuckenia pectinata*, and *Potamogeton pusillus*. During the summer growing seasons, clear-water states are characterized by lower concentrations of epilimnetic TP and Chl *a*, compared with turbid states (Fig. 3). Throughout both the clear and turbid

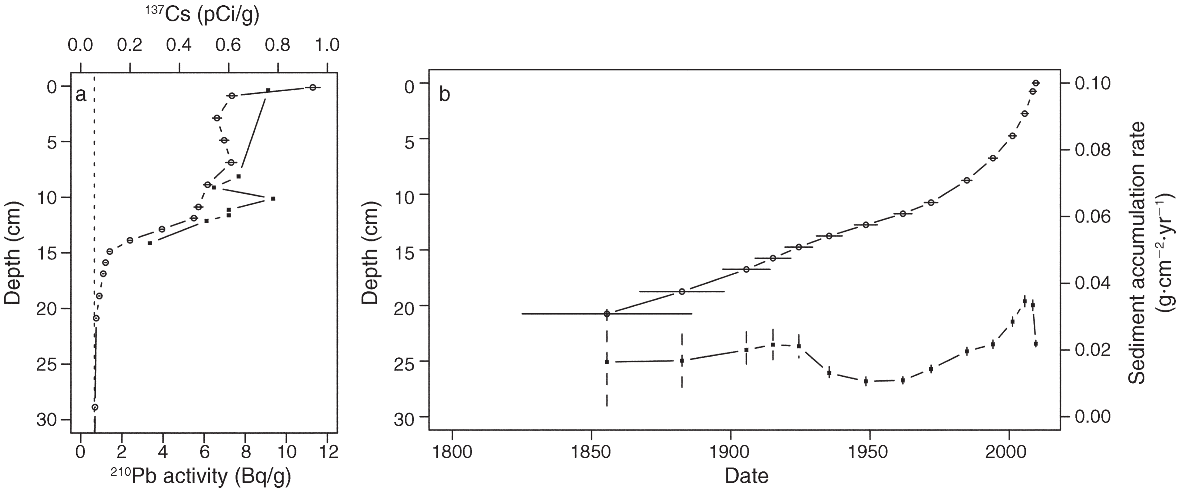

FIG. 4. Results of ^{210}Pb dating showing (a) the total ^{210}Pb (circles) and ^{137}Cs (squares) inventories with depth, where the dashed line represents the ^{210}Pb background activity, and (b) the modeled sediment ages (circles) and calculated sedimentation rates (black squares) with error bars showing ±SD.

states, Lake Christina remains eutrophic and phytoplankton growth appears to be P limited, based on TN:TP$_{molar}$, which is >45 from 1985 to present (Table 1; Elser et al. 2009). During clear states, large-bodied *Daphnia* (*D. pulex* and *D. galeata*; Hanson and Butler 1994*a*) establish and *Bosmina* spp. (mainly *B. longirostris*) decline due to competition (Fig. 3). As the lake begins to transition back to a turbid state, *Bosmina* spp. dominate the cladoceran community, along with *Chydorus* spp. (Hanson and Butler 1994*a*).

Geochronology and sediment accumulation

In core CRWB09 supported ^{210}Pb (background) was reached at a depth of 21 cm and the average dry-mass sediment accumulation rate for the core site is 0.019 g·cm^{-2}·yr^{-1} (Fig. 4a). The average sediment accumulation rate is based on estimated rates from the section of the core where organic content is relatively constant and there are no dramatic changes in the dry bulk density of the sediment (below 15 cm). The average sediment accumulation rate and dry bulk density were used to extrapolate the ^{210}Pb model to 1800 (Binford 1990). While the onset of ^{137}Cs is evident, no clear peak could be defined to confirm the 1963 age horizon (Fig. 4a), possibly due to migration within the sediments and poor binding of ^{137}Cs to the sediments, as reported in similar lake systems (Brenner et al. 2006). Comparable sedimentation between both cores was confirmed by analysis of dry bulk density (g/cm^3) on both cores at the same depths ($r^2 = 0.98$, $P < 0.001$, df = 18) and thus we confidently applied the age–depth model to core CRWA09.

The sediment accumulation rate (SAR) is relatively stable from the 1850s to the 1930s, when it decreases and then it slowly increases after 1960 (Fig. 4b). The sediment of Lake Christina is dominated by autochthonous calcite precipitation (Hanson et al. 1990), comprising ~60% by dry mass. Multiple linear regression analysis with the percent sediment composition showed that SAR is positively influenced by the deposition of organics ($r = 0.81$, $P < 0.001$, df = 19), and inversely correlated to carbonates ($r = -0.84$, $P < 0.001$, df = 19) or the minerogenic fraction (not significant).

Organic matter source

Both the C:N and δ^{13}C of organic matter have been useful in studies of lake sediments to determine the provenance of the organics (Kaushal and Binford 1999, Meyers and Teranes 2001). Modern *Stuckenia pectinata* (sago pondweed) had a C:N$_{atomic}$ of 20.1 ± 0.2 (mean ± SD) and a δ^{13}C of −11.5 ± 0.03‰, whereas *Myriophyllum sibiricum* (shortspike water milfoil) had a C:N$_{atomic}$ of 23.6.1 ± 3.2 and a δ^{13}C of −10.8 ± 0.9‰. Modern phytoplankton had a C:N$_{atomic}$ of 10.5 ± 1.1 and a δ^{13}C of −14.6 ± 0.7‰ (Fig. 5). The sediment organic matter has a C:N$_{atomic}$ ranging from 8.5 to 16.2 (mean: 11.2 ± 2.1) and a δ^{13}C ranging from −8.6 ‰ to −19.4‰ (mean: −14.2 ± 2.9‰). A biplot of C:N$_{atomic}$ and δ^{13}C shows that sediment organic matter falls within the range of modern primary producers and there has been a general transition from predominately SAV to phytoplankton (Fig. 5).

Recent sedimentary records (1980–present)

The trends in *Bosmina* abundance recorded in both sub-fossil and monitored water column samples are very similar ($r = 0.8$, $P = 0.03$). The lowest *Bosmina* densities are present during the clear states and higher densities during the turbid (Fig. 6). Additional remains of the zooplankton communities were observed in our sediment samples (e.g., *Chydorus* spp.), however only *Bosmina* remains were of sufficient density for quantitative analysis and directly correlated with contemporary sampling. Profiles of sedimentary TP and TChla

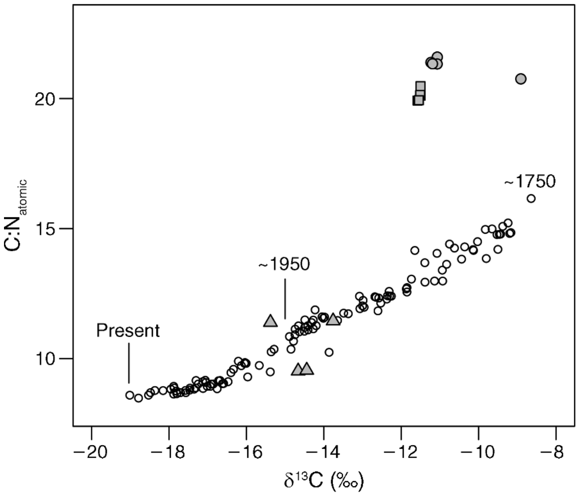

FIG. 5. Biplot of the C:N$_{atomic}$ and δ^{13}C of organic matter in modern algae (shaded triangles) and macrophytes (*Myriophyllum sibiricum* [shortspike water milfoil], shaded circles; *Stuckenia pectinata* [sago pondweed], shaded squares) and sediment (open circles). The approximate trajectory of the sediment core is highlighted by age markers.

trends since 1980 do not show any clear response to the alternate states of the lake. TChla shows little variability from 1980 to 2000, after which concentrations begin to increase monotonically. Concentrations of TP show some correlation with epilimnetic TP post-2000, however this is based on a single sample at approximately 2002 and it would be an over-interpretation to conclude any correlation between epilimnetic and sediment measurements. In general the trends in sediment TP show a slight increase in the early 1980s, with little overall change since the 1990s.

Long-term sedimentary records (1800–present)

All of the sediment proxies used in this study show a single dramatic shift in the ecology of Lake Christina occurring at approximately 1950 (±4 yr for dating uncertainty). Given the unprecedented responses of all our proxy data, at least within the context of the past 200 years, we consider this to be a regime shift into a modern period where anthropogenic drivers dominate how the lake ecosystem functions (Fig. 7). Trends in TChla and TP closely mimic each other, beginning to increase approximately 10 years prior to the regime shift. The accumulation of TOC is very stable from $\sim$1800 through 1920, when it decreases until 1950 and then increases well beyond historical rates starting in the late 1950s. The turnover of sub-fossil diatom assemblages is summarized by the DCA axis 1 (31% variance explained; Fig. 7e); the community is relatively stable from $\sim$1800 to 1950 and composed of small colonial (*Staurosirella pinnata*, *Pseudostaurosira brevistriata*, and *Fragilaria capucina*) and solitary (*Navicula cryptotenella* and *N.* cf. *libonensis*) benthic species, and the epiphytic taxa (*Cocconeis placentula* and *Gomphonema angustum*) (Fig. 8). The shift at 1950 is the only statistically significant change in the assemblages, as compared to a random broken-stick model. Following 1950 the communities include significant percentages of tychoplanktonic species (Fig. 8), namely, *Fragilaria tenera* and *Aulacoseira ambigua*. The sub-fossil *Bosmina* densities increase dramatically post-1950, however unlike the other proxies there is a response to the turbid – clear state manipulations, and densities drop to near historic levels during the clear-water states (Fig. 7f). The sediment record over the last 200 years shows the stable historic period where a clear-water, macrophyte-dominated state predominates, with a regime shift at 1950 into a managed period where turbid, phytoplankton-dominated states are predominant (Fig. 7g).

DISCUSSION

Lake response to biomanipulations

Since the 1960s, three top-down ecosystem manipulations in turbid Lake Christina have induced temporary shifts to a clear state, lasting 5–10 years, followed by a return to a turbid state (Fig. 3). It is clear that the fish kills of largely planktivores and benthivores induced a trophic cascade, indirectly affecting summer primary production and lake water turbidity (Hanson and Butler 1994*a*). Of particular importance was the establishment of large bodied *Daphnia* spp. (*D. galeata* and *D. pulex*) that grazed summer phytoplankton crops and affected the summer algal bloom composition pre- and post-manipulation (Hanson and Butler 1994*a*). In response to the increase in *Daphnia* densities, *Bosmina* abundance declined during the temporary clear states owing to direct competition for resources. The response of *Bosmina* densities is captured accurately by sub-fossil remains in the lake sediments, adding additional confirmation to the reliability of the sediment record (Fig. 6). With the increase in summer *Daphnia* abundance, chlorophyll *a* concentrations in the water column begin to decrease (Fig. 3). There is also a reduction in summer turbidity owing directly to the reduction of phytoplankton ($\sim$15–40% of the seston) and associated change in calcite precipitation ($\sim$10–60% of the seston) due to a reduction in CO_2 demand (Hanson et al. 1990).

While the periods of manipulation induced a strong epilimnetic response in summer primary production (Hanson and Butler 1994*a*, *b*), the annual primary production was unaffected by the temporary shift from a turbid to clear state, evidenced by sedimentary records of TChla, biogenic silica (data not shown), and TOC MAR (Fig. 7). This finding is consistent with data from a number of shallow lakes in western Minnesota (including Lake Christina) suggesting that contemporary net ecosystem production does not vary between turbid and clear states during the summer (Domine 2011). The role of benthic production should be considered as an explanation for this observation. Water quality monitoring data for Lake Christina show that

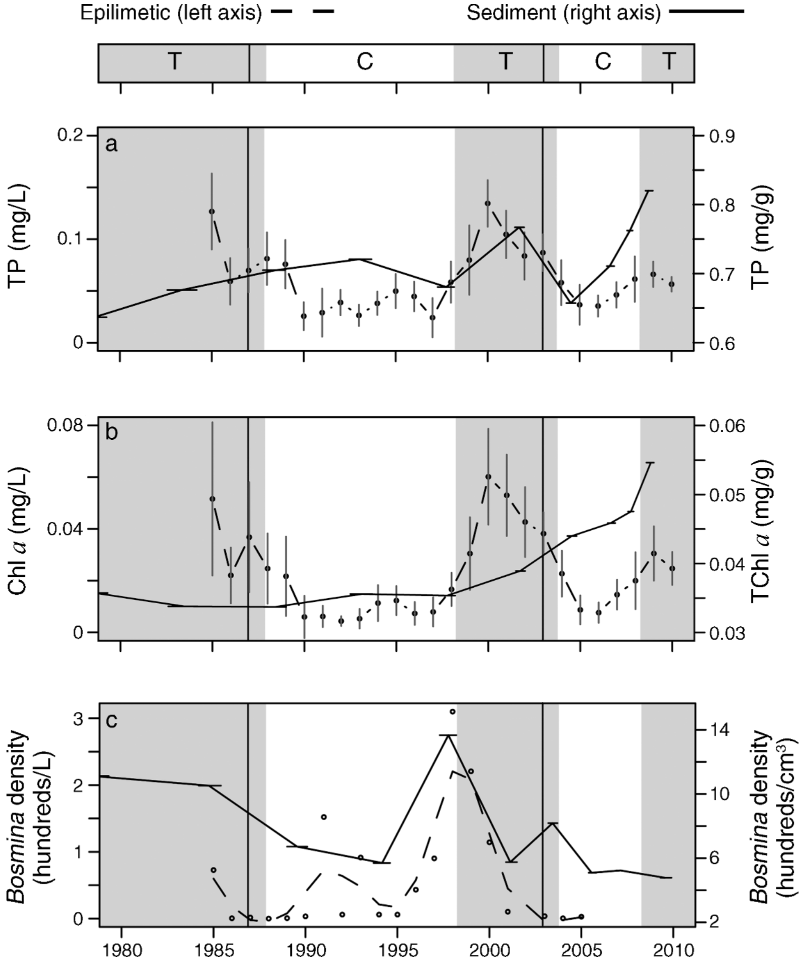

FIG. 6. Modern epilimnetic (dashed line) and paleolimnological (solid line) data for (a) total phosphorus, (b) total chlorophyll *a* (TChl *a*), and (c) *Bosmina* density over the period from 1980 to present. Vertical black lines through each panel show the manipulations of 1987 and 2003. Modern data represent a mean of five sampling sites throughout the open water season ($n = 20$–56) with standard deviations and linear trend as a dashed line. Modern *Bosmina* densities are taken from the monitoring station closest to the core site, and linear trends are shown through a LOWESS smooth at a span comparable to the sediment intervals (~5 years). Sediment records are shown as bars spanning the date of the sediment interval and solid trend lines. Turbid states (T) are shaded gray, and clear states (C) are white.

light is rarely limiting to benthic algae (i.e., PAR > 1%; Table 1; Vadeboncoeur et al. 2008) in either a turbid or clear state, over a range of [TP] (0.03–0.13 mg/L). As a result, sub-fossil diatom communities throughout the sediment record are dominated by benthic species, ranging from 63% to 92% abundance (Fig. 8). Therefore, benthic primary production must be an important contributor to whole-lake primary production shaping the trends in sediment TChla in both the turbid and clear state, and a component that is not captured by summer epilimnetic sampling.

Historical lake regime

The Lake Christina ecosystem was significantly different during the 1800s and early 1900s, when compared to the post-1950 period (Fig. 7). Sedimentary measures of primary production (TChla and TOC MAR) and trophic status (TP) suggest a less productive ecosystem with lower nutrient concentrations. The source of organic matter in the sediments during this historical period is most attributable to macrophyte remains over an algal source. From surveys of large populations of Canvasback Ducks that depend on *Stuckenia pectinata* (sago pondweed) as a critical food source (Smith 1946), we can infer that the macrophyte community of Lake Christina was dominated by this plant and more than likely the lake was in a clear-water state into the mid-1940s. Diatom communities in the pre-1950 period are dominated by small, benthic, colonial species, with low abundances of taxa (*Cocconeis placentula* and *Gomphonema angustum*; Fig. 8). The densities of *Bosmina* remains during this period are similar to those present during the temporary macrophyte-dominated clear states following manipulations.

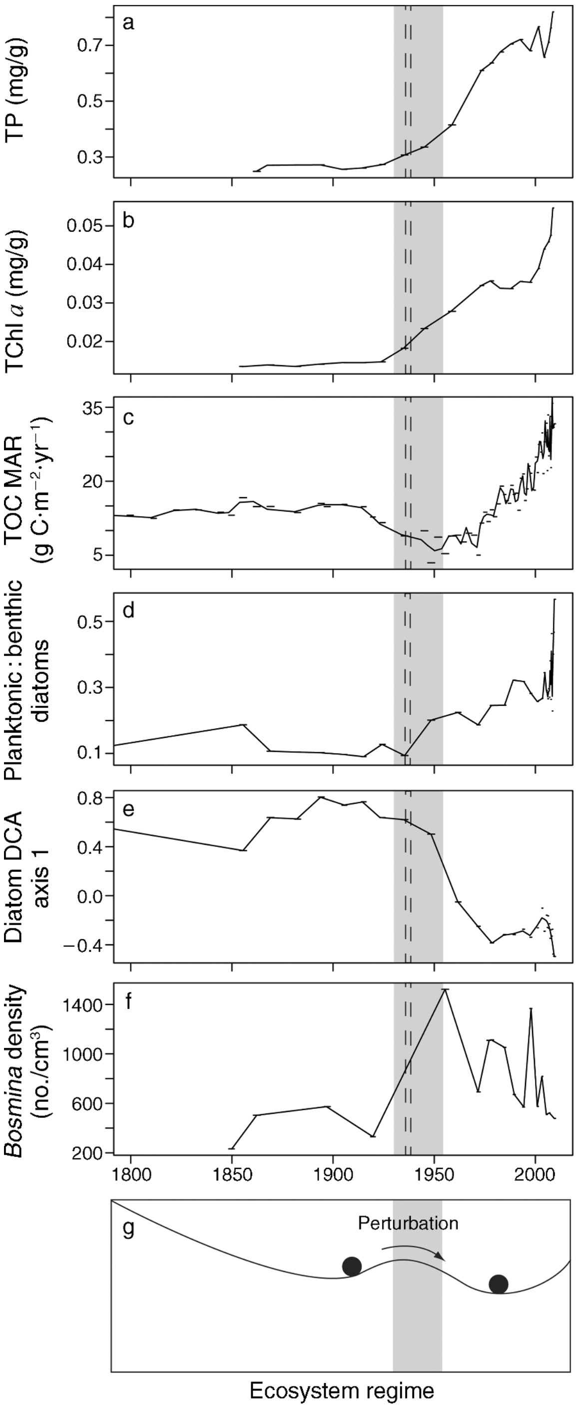

FIG. 7. Multiple sediment core proxies of (a) lake trophic status (TP), (b, c) primary production (TChl *a* and total organic carbon mass accumulation rate [TOC MAR]), and (d–f) paleoecological sub-fossils (diatom assemblage turnover [DCA axis 1], planktonic : benthic diatoms, and *Bosmina* remains) over the last 200 years in Lake Christina. (g) The theoretical stability landscape that describes the perturbation to the lake, causing a regime shift into the modern managed period. The dashed line through each panel represents the construction of a dam with the sediment age dating error (~4 years). The shaded area is the period of the regime shift.

Settlement of the Lake Christina catchment began in earnest in the late 1800s as homesteads and farms were established. However, there is no indication of an immediate post-settlement impact to the lake ecosystem. The paleoecological data indicate that prior to human settlement and into the early 1900s, Lake Christina was a clear-water, macrophyte-dominated lake with lower primary production than today.

Multiple drivers of long-term ecosystem change

There is a single significant regime shift in the 200-year sedimentary record of Lake Christina that occurs at approximately 1950 (Fig. 7). This perturbation of the ecosystem represents the transition of the lake into the modern managed period where a turbid state predominates. The record of TP in sediments begins to increase approximately 10 to 20 years prior to the lake moving into the modern managed period. In accordance with the theory of alternative stable states, a lake should be past some threshold of eutrophication in order for algae to be the dominant primary producer. We consider two possibilities for increased nutrient loading to the lake during the late 1930s through the 1940s, which are not mutually exclusive: (1) increased agricultural activities and changes to the surrounding landscape, and (2) within-lake changes in nutrient cycling from waterfowl. Aerial photographs from 1938 show that approximately 80–90% of the lake catchment is cultivated land, with the remaining either wetlands or small woodland areas. The farms were small and diverse, growing small grains (e.g., oats, wheat) and alfalfa, and raising livestock. Common practice in the late 1930s and 1940s was to stockpile manure through the year for spreading during the spring, which would lead to direct and indirect nutrient additions to the lake. Alternately, or in addition, the internal nutrient loading by migratory waterfowl during the early 1940s, when populations were probably close to 400 000 total ducks and coots (Ordal 1966), could have mobilized formerly refractory (SAV tubers) and allochthonous (birds feeding outside the lake) nutrient pools through excretion from the birds. For example, current total waterfowl populations (600 000 in 1994; Table 1) could theoretically supply 114 kg P/d (Manny et al. 1994), which is an areal loading rate of 2.1 kg $\mathrm{P \cdot ha^{-1} \cdot yr^{-1}}$ (over a 30-day migratory period), and is comparable to export coefficients from agricultural land (1.9 kg $\mathrm{P \cdot ha^{-1} \cdot yr^{-1}}$; Almendinger and Murphy 2007). The sedimentary [TP] provides evidence that Lake Christina underwent eutrophication prior to the transition into the modern managed period; the likely mechanism was through nutrient loading from the surrounding catchment and/or waterfowl.

In 1936, a dam was built on the main outlet of the lake and on the outlet of the adjoining downstream Pelican Lake. Over the course of the next decade, the water levels of Lake Christina increased by 0.25–0.75 m, primarily in response to the dam on Pelican Lake (Appendix: Fig. A1). This increase in water level

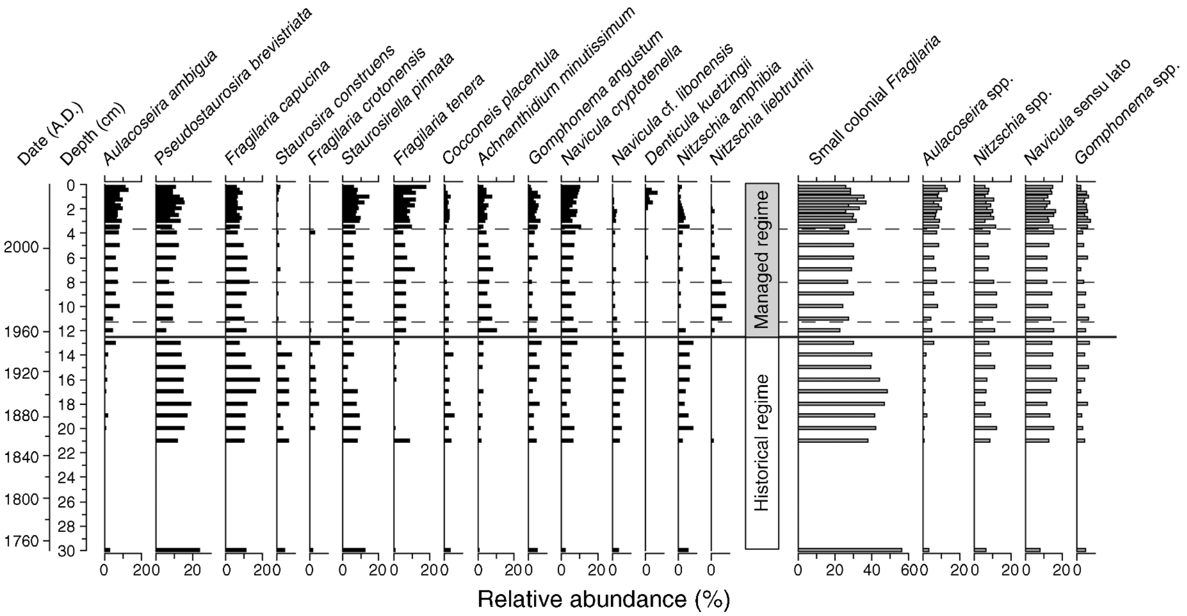

FIG. 8. Sub-fossil diatom assemblages in Lake Christina since ~1750 AD. Individual species >5% abundance are shown as black bars, and genus-level summaries are shown as gray bars. Dashed lines mark the lake manipulations, while the solid line marks the significant shift in diatom communities from the historical period.

approximately doubles the depth of the main basin of Lake Christina, even when considering the amount of sediment infilling since 1940 (~0.15 m), but did not increase the area of the lake basin (T. Carlson, *personal communication*). By the late 1940s, the water level of Lake Christina was comparable to today. In response to the increasing water level, the relative abundance of tychoplanktonic diatoms increased, and the assemblages significantly changed. Into the mid-1950s *Bosmina* spp. increased, which suggests a loss in macrophyte communities based on observed high *Bosmina* densities during turbid states (Fig. 6). The loss of macrophytes in response to hydrologic fluctuations is not novel and similar losses have been documented with relatively modest increases in water level (Wallsten and Forsgren 1989), while decreases in water levels have encouraged the establishment of macrophytes (Van Geest et al. 2007). Successful biomanipulations in Lake Christina have demonstrated the indirect and direct impact that top-down pressures by planktivorous and benthivorous fish have on the presence of macrophytes. The change in hydrology must have decreased the prevalence of natural winter kills of fish, further suppressing the macrophyte communities.

Climatic variability alone does not appear to induce a regime shift in Lake Christina. The construction of the dam occurs at a time when the region was emerging from the multi-annual drought of the 1930s, where increases in regional humidity contributed to the increasing water level (Schubert et al. 2004, Cook and Krusic 2008). Despite the depth of Lake Christina being influenced mainly by a dam on downstream Lake Pelican for the last 70 years, there is a statistically significant portion of the water level variation explained by climate, summarized by the Palmer Drought Severity Index (PDSI; $r = 0.56$, $P < 0.001$, df $= 51$; Appendix: Fig. A1). During 20th-century droughts when the PDSI is similar to the 1930s (e.g., 1976 and 1988–1989) the water level of Lake Christina does not respond as dramatically, suggesting that the dam has decreased how sensitive the lake level is to drought, and there is no distinct ecological response. Droughts of the early 1820s and 1860s during the historical period of the lake most likely decreased the water level of the lake, but again there is no detectable ecological response in the sediment record. Therefore, it appears that the lake level was influenced by the increase in humidity at the end of the dust bowl, but the construction of the dam is what sustained a high water level under nutrient-enriched conditions and induced the regime shift.

In summary, the regime shift in Lake Christina was a consequence of multiple stressors over a ~30-year period in the mid-1900s (Fig. 7). The eutrophication that began in the 1930s to 1940s promoted higher phytoplankton abundance. This may have resulted in a higher fish biomass favoring fewer piscivores and greater numbers of planktivores and benthivores (Jeppesen et al. 2000). Reduced chances of natural winterkill due to greater water depths following construction of the dam and increased annual rainfall sustained higher biomass of undesirable fish, favoring the turbid state. The synergy among eutrophication, dam construction, and climatic variability conspired to cause the regime shift to a period where a turbid lake state persists.

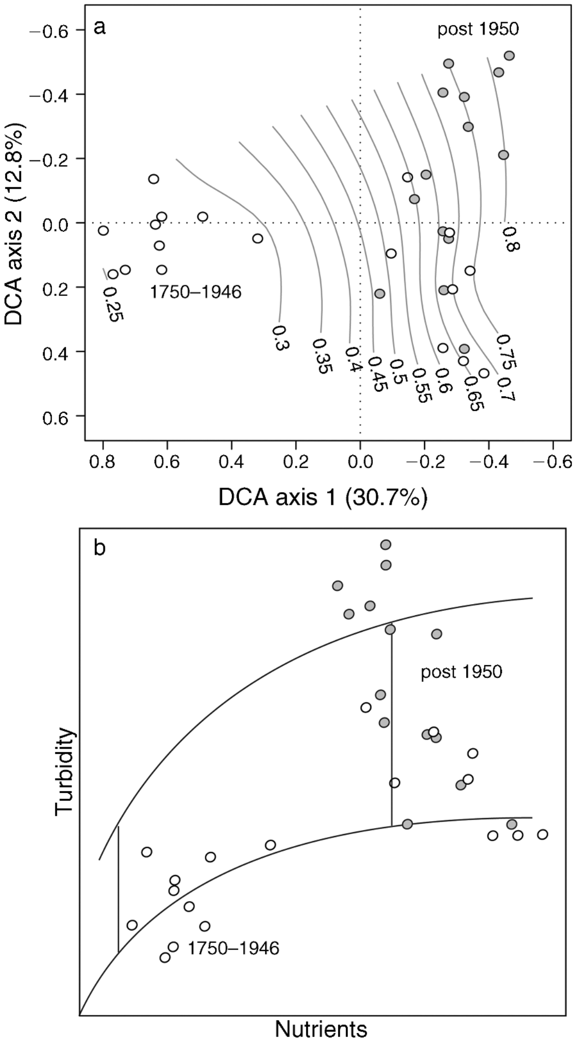

FIG. 9. (a) DCA of sub-fossil diatom assemblages with the sediment TP concentration for each corresponding interval passively contoured by thin-plate splines over ordination space. Shaded circles are intervals when Lake Christina is in a turbid state, while open circles are clear state. (b) Ordination space from panel (a) overlain by the theoretical model for nutrient-driven regime shifts (sensu Scheffer and Carpenter 2003).

Alternative stable state theory, regime shifts, and lake management

Over the last 200 years, the Lake Christina ecosystem has undergone a regime shift from a historically stable period where a clear-water state was dominant to a period where a turbid state persists. The functioning of the lake ecosystem is now managed and biomanipulated clear-water states are unstable. This long-term trajectory of the lake and the history of biomanipulations from Lake Christina help demonstrate the concept of stability "landscapes" (sensu Scheffer and Carpenter 2003) and alternative stable states, and effectively link theory to observation. In an unconstrained ordination of the sub-fossil diatom communities with the sediment TP data passively overlain, the main direction of diatom community turnover, from a stable, clear state (~1750–1946) to a period where the turbid state persists (post-1950), is along DCA axis 1, which coincides with an increase along the TP gradient (Fig. 9a). During the period of ~1750–1946 there is a low influence by external conditions (nutrients) and the ecosystem is relatively stable. As the influence of nutrients on the lake increases at the end of the 1930s through the late 1940s, the stability landscape begins to change and Lake Christina becomes more susceptible (unstable) to a catastrophic regime shift or perturbation. This regime shift takes place during the mid-1950s when water levels are high, macrophytes are lost and nutrients are sufficiently elevated to promote phytoplankton dominance, reducing the stability of the historical clear-water state, and pushing the lake into the modern managed period dominated by a turbid state (Fig. 9b). In the modern managed period, Lake Christina undergoes three top-down manipulations pushing the ecosystem into a temporary or unstable clear state. The sediment record shows that each of these manipulations was not associated with reductions in nutrients, whether catchment-derived or internally cycled. Instead, each biomanipulation moves the ecosystem back and forth on a turbidity gradient, but without the reduction of nutrients to limit algal production a return to an ecosystem similar to the stable historical clear state is not possible (Fig. 9).

Managed lake ecosystems are commonplace in today's landscapes. The future rehabilitation of Lake Christina is now reliant on a hydrologic drawdown system to emulate natural variability in water levels and induce periodic winterkill of planktivorous and benthivorous fish. Given the lake's history of biomanipulations, we know this approach will be successful in the short term for inducing clear-water states. However, our results indicate that it is unlikely Lake Christina will return to the persistent or stable clear state that characterized the historic ecological period. Similar findings in other studies of biomanipulations indicate that long-term improvements may not be sustainable without additional interventions (e.g., nutrient reduction; McQueen 1998, Jeppesen et al. 2007). In an attempt to reduce nutrient inputs, considerable efforts initiated in the 1980s by the Minnesota Conservation Reserve Program, U.S. Fish and Wildlife Service, and Minnesota Department of Natural Resources have reduced the percent cover of cultivated land and increased the number of wetlands in the catchment. Despite these efforts the lake has remained eutrophic, suggesting internal nutrient cycling may be important. The status of the lake as an important waterfowl staging area continues to capture the interest and willingness of the public to support management efforts, where the short-term improvement justifies the cost of biomanipulations (Hansson et al. 1998). Lake Christina is a prime example of an ecosystem forced by multiple stressors into a new long-term managed period, where manipulated clear-water states are temporary, managed features.

Acknowledgments

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SUPPLEMENTAL MATERIAL

Appendix

A figure showing water level data for Lake Christina since 1936, correlation with instrumental Palmer Drought Severity Index (PDSI) data, and regional tree-ring reconstructed PDSI data over the last 200 years (*Ecological Archives* A022-077-A1).