

ORIGINAL ARTICLE

Long-Term Stability of Macrophyte Dominance Triggered by Common Carp Removal from a Temperate Shallow Lake

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ABSTRACT

Many ecosystems can abruptly shift between states, and shallow lakes are a classic example. Biomani-
pulation via the removal of benthivores can shift
a shallow lake from a turbid to a clear-water
macrophyte-dominated state, but the limited
number of long-term studies indicates that persis-
tence in this state rarely lasts beyond 5–10 years.
We analyzed 12 years of pre-removal (1996–2007)
and 17 years of post-removal (2008–2024) data to
assess the ecological impacts of a common carp
(*Cyprinus carpio*) removal from Lake Wingra, a
shallow eutrophic lake in Madison, Wisconsin,
USA. Summer water clarity abruptly increased
following the winter 2008 carp removal, resulting
in a 64% increase in mean Secchi depth in post-
removal summers and a major expansion of the
littoral zone. Fast growing submerged macrophytes
(for example, *Ceratophyllum demersum* and invasive
Myriophyllum spicatum) rapidly expanded into dee-
per zones, reaching the maximum colonization

depth of 3.96 m within four summers. Post-re-
moval nutrient concentrations declined by 24–34%
and became more correlated with precipitation,
suggesting a shift from internal to external regula-
tion of nutrient loading. Three likely interacting
mechanisms for maintaining water clarity include
predation by centrarchids maintaining low carp
populations, the high and stable coverage of sub-
merged macrophytes, and abundant filamentous
algae that provide an additional nutrient sink.
However, high biomass of invasive species and fil-
amentous algae can degrade ecosystem services and
function, and increased variability of precipitation-
driven nutrient inputs may destabilize the macro-
phyte-dominated state in the future. We demon-
strate with long-term data the sustained shift of a
shallow eutrophic lake out of the turbid state with a
single biomanipulation.

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the carp reduction project. All authors contributed to study design and
manuscript writing.

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HIGHLIGHTS

- Improved water clarity and high macrophyte abundance were sustained for 15-years after a lake carp removal.
- A consequence of shifting to a macrophyte dominated state was the dominance by invasive Eurasian watermilfoil and years of high coverage of filamentous algae.
- Post carp removal, precipitation played a dominant role in interannual variation in water clarity and biological responses.

Key words: Abrupt shift; Biomanipulation; *Cyprinus carpio*; Lake Wingra; Macrophytes; *Myriophyllum spicatum*; Shallow lake.

INTRODUCTION

In ecosystems, alternative stable states arise when distinct sets of conditions are maintained by internal feedbacks despite similar external environments. Examples in nature include: coral reefs, shifting from coral to algal dominance (Norström and others 2009; Hughes and others 2017) or forests shifting to grasslands due to fire frequency (Calder and Shuman 2017). These transitions may take place gradually through time, or abruptly, and result in alternative stable states, with very different ecosystem structure, functions, and services. Abrupt ecological transitions can also occur without alternative stable states. In such cases, the ecosystem undergoes a continuous but rapid shift rather than a discontinuous (that is, catastrophic) shift between basins of attraction (Ratajczak and others 2018). For both types of shifts, positive feedbacks reinforce the ecosystem state, contributing to the sharpness of the transition. Understanding the mechanisms and feedbacks that lead to the persistence of these states is increasingly important for predicting and managing ecosystem response to environmental change as climate change continues to accelerate (Biggs and others 2018; Ratajczak and others 2018; Turner and others 2020).

A classic example of alternative stable states is the response of a shallow lake to eutrophication. Shallow lakes most commonly exist as either clear water with extensive beds of macrophytes or turbid water with high phytoplankton biomass (Scheffer and others 1993; Scheffer and van Nes 2007). Theory suggests clear-water conditions will persist

until a stressor (for example, nutrient enrichment) reaches a threshold, triggering an abrupt shift to turbid conditions. Turbidity from phytoplankton biomass attenuates light in the water column, effectively shading out macrophytes and decreasing their growth. Without rooted macrophytes, bottom sediments are more prone to resuspension, leading to internal phosphorus (P) loading and additional light attenuation (Scheffer and others 1993; Søndergaard and others 2003). This positive feedback loop can be hysteretic, in which the ecosystem becomes stable in the turbid state, making it resistant to shifting back to the clear-water state, even with reductions in nutrient loading (Scheffer and others 1993). A strong perturbation is necessary to overcome the resilience associated with a high phytoplankton state.

Invasive common carp (*Cyprinus carpio*; hereafter ‘carp’) are benthivorous fish that reinforce strong positive feedback loops in the turbid state of shallow lakes (Jackson and others 2010; Weber and Brown 2011). Carp increase water column P and nitrogen (N) through bioturbation of benthic sediments during foraging and through excretion (Lamarra 1975; Huser and others 2016). The foraging can cause bottom sediments to become unconsolidated and thus more prone to wind-induced resuspension (Zambrano and others 2001; Lin and Wu 2013). Their foraging activity can also uproot macrophytes, thereby increasing available nutrients when the vegetation subsequently decomposes (Crivelli 1983). Furthermore, carp alter top-down processes by feeding on benthic invertebrates (Zambrano and others 2001) and creating conditions (increased suspended sediments) that impede algal grazing by larger zooplankton (Hart 1988; Kirk 1991; Schrage and Downing 2004). Their early maturation, rapid growth, longevity, and ecological plasticity make carp populations difficult to control (Weber and Brown 2009).

Carp removals (biomanipulations) are able to perturb shallow lake ecosystems from a turbid state back to a macrophyte-dominated state (Hansson and others 1998; Bergman and others 1999; Søndergaard and others 2008; Huser and others 2022). However, most studies focus on short-term responses (van Donk and van de Bund 2002; Søndergaard and others 2007; Jeppesen and others 2012), with few documented cases of long-term persistence of the clear-water state. The limited number of long-term (> 10 years) investigations suggests that gains in water clarity due to biomanipulation efforts are often reversed after 5–10

years due to the return of benthivorous fish, delayed colonization by macrophytes, or a persistent nutrient supply (either internal or external) (Søndergaard and others 2008; Bernes and others 2015). Low nutrient availability in the water column is central to the long-term stability of the macrophyte-dominated state (Jeppesen and others 1990; Scheffer and others 1993; Meijer and others 1994). Competition for light and nutrients between floating-leaf plants, filamentous algae, and phytoplankton, may reduce nutrient availability in the water column and help maintain low phytoplankton populations (Iacarella and others 2018). Climatic changes, such as more frequent precipitation,

could destabilize the macrophyte-dominated state by intensifying external nutrient and organic matter loading (Jeppesen and others 2007; Søndergaard and others 2008). This is especially relevant for the Upper Midwest region of the USA, where the frequency of large rainfall events has increased over the past 60 years (Villarini and others 2013).

Here, we evaluate the long-term response of a shallow eutrophic lake to a single biomanipulation (carp removal). We present 12 years (1996–2007) of data pre-intervention and 17 years (2008–2024) of data post-removal from Lake Wingra, a shallow eutrophic lake in Madison, Wisconsin, USA. We investigated whether the carp removal led to an

Table 1. Hypothesized Effects and Generalized Findings of Carp Removal on Secchi Depth, Nutrients, Chlorophyll a, Total Particulate Matter, Macrophyte Biomass and Diversity, and Filamentous Algae in Lake Wingra

Response variable	Expected response	Rationale	Finding
Secchi depth (light penetration)	Immediate increase in water clarity post-carp removal	Decreased carp foraging will reduce the resuspension of sediment in the water column	Immediate increase in Secchi depth that was sustained from 2008 through 2024
Total nitrogen (TN)	Decrease in surface TN concentrations immediately following removal	Reduction in carp bioturbation and excretion decreases nitrogen release from sediments. Enhanced macrophyte growth and microbial activity may promote uptake and denitrification	TN decreased after removal but was later variable with some wet summers near pre-removal levels
Total phosphorus (TP)	Decrease in surface TP concentrations immediately following removal	Carp disturb sediments and excrete phosphorus, increasing water column concentrations. Removal reduces sediment resuspension and internal loading	TP decreased after removal but was later variable with some wet summers near pre-removal levels
Chlorophyll a	Reduction in chlorophyll a as a proxy for pelagic phytoplankton biomass	Initially no change due to high light and external nutrient inputs; decrease expected as macrophytes reestablish and there is competition for light and nutrients	Chlorophyll a concentrations in the middle of the lake were similar to pre-removal concentrations
Total particulate matter (TPM)	Decrease in TPM following removal	Carp disturb sediments and lack of macrophytes promotes wind resuspension	TPM decreased after carp removal
Macrophyte biomass and diversity	Greater colonization depth, increased biomass, initial diversity rise followed by stabilization or decline	Improved water clarity and habitat support recolonization. Dominant species may limit long-term diversity	Maximum colonization depth reached within four years. Biomass increased, dominated by Eurasian watermilfoil and Coontail; no change in species diversity
Filamentous algae	Greater filamentous algal biomass associated with macrophyte re-establishment	Periphyton production can be high in eutrophic macrophyte-dominated lakes	Filamentous algal biomass increased in 2008 and has high variability year to year. Highest in years with high zooplankton densities

abrupt shift in ecosystem state, as evaluated by expected shifts in water clarity (Secchi depth), nutrients and chlorophyll *a* concentrations, total particulate matter, macrophyte and filamentous algae biomass, and macrophyte colonization depth (Table 1). We also explore the ecosystem dynamics that changed post-carp removal that may contribute to long-term persistence of the macrophyte-dominated state.

METHODS

Site Description

Lake Wingra is an urban headwater drainage lake that receives inflow from stormwater infrastructure, springs, and groundwater. The lake has one outflow stream on the eastern side that is dammed to regulate water level. The lake has a surface area of 138.5 ha, a mean and a maximum depth of 2.7 and 4.0 m, respectively, and a mean water residence time of ~0.44 years (Seyb and Randolph 1977). The lake is polymictic and can stratify for periods of hours to weeks but does not sustain thermal stratification throughout summer (Kimura and others 2016). The mean duration of ice cover on Lake Wingra is 109 days (2000–2023) typically from December to March.

Carp were first introduced into the Yahara River chain of lakes in the late 1800s (Lathrop and others 1992), and by 1913, carp were reported to “abound” in Lake Wingra (Cahn 1915). Efforts to reduce the carp population began as early as the 1930s. Carp were greatly reduced during the mid-1950s (Neess and others 1957; Baumann and others 1974). How long their densities remained low is not certain, but water clarity was 0.6–0.7 m in 1970 (Kluesener 1972). In March 2008, 23,600 kg of carp was removed by seining under the ice (Lathrop and others 2013; Vander Zanden and others 2024). Otolith aging of a subsample of captured carp indicated they were > 35 years old (DNR unpubl. data). An additional 1,500 kg was removed in March 2009 after ice-out. Later in 2009, Lake Wingra’s v-notch weir outlet dam was replaced with a spillway to deter carp migration into the lake while maintaining the same water level (Lathrop and others 2013). The removal reduced the carp biomass by 181 kg ha⁻¹ to relatively low densities in Wingra. No further carp removals have occurred since 2009.

Time Series Data

Time Series of Limnological Data

Limnological monitoring of Lake Wingra has been conducted by the North Temperate Lakes Long-Term Ecological Research (NTL-LTER) program since 1996 (Table S1) at the deep hole on the western side of the lake (43.053, -89.425). Time series of water quality parameters include: water clarity (Secchi depth) (Magnuson and others 2025b), chlorophyll *a* as a proxy for phytoplankton biomass (Magnuson and others 2024b), total unfiltered nitrogen (TN), total unfiltered phosphorus (TP) (Magnuson and others 2025c), and total particulate matter (TPM) (Magnuson and others 2022c).

Biweekly vertical profiles of photosynthetically active radiation (PAR) in Lake Wingra began in 2021 (Magnuson and others 2025a). We used 20 co-occurring measurements to compute the relationship between Secchi depth and photic zone depth (1% light availability). The photic zone depth is approximately 3.3x the Secchi depth in June through August in Lake Wingra (Figure S1).

For surface nutrients, we combined results from samples analyzed by NTL-LTER and the Wisconsin State Lab of Hygiene (WSLH) and calculated the mean when two samples were collected on the same day. Prior to 2015, WSLH TN was calculated as the sum of Kjeldahl nitrogen and nitrate + nitrite. For chlorophyll *a*, samples were extracted in methanol, measured with a fluorometer, and corrected for pheophytin. For each sampling date, we included both surface and integrated (0–2 m) measurements and averaged across any replicate samples. Samples were collected roughly fortnightly during the summer open-water season (June to August), and therefore most water quality variable has 6–7 measurement dates per summer. An exception is 2020, when sampling was curtailed. For summary analyses at the annual scale, 2020 was removed from statistical analyses due to unrepresentative sampling efforts.

For chlorophyll *a*, we used fluorometric data uncorrected for pheophytin. This choice was made as samples after 2020 had a noticeable shift in magnitude when corrected for pheophytin, which may be due to laboratory holding times. TPM was sampled monthly from 2000 to 2013 from 0 to 2 m depth. Lake water was pumped through a pre-weighed 0.45-μm membrane filter. The filter was then dried at 60°C and weighed on an analytical balance to calculate particulate mass.

Zooplankton community data for Lake Wingra are available only from 2007 to 2018, and therefore changes before and after carp removal cannot be compared. Post 2007, NTL-LTER enumerated zooplankton densities at multiple time points every summer ($n = 2$ for 2007–2008, $n = 4$ for 2009–2010, and $n = 3$ for 2011–2018) from a subsample of a vertical net tow with a 30-cm-diameter opening and 80 μm mesh (Magnuson and others 2024a). We subset zooplankton into two groups: 1) all *Daphnia* species (*Daphnia pulicaria*, *Daphnia retrocurva*, *Daphnia mendotae*, *Daphnia parvula*, *Diaphanosoma birgei*, *Daphnia* (genus only), and 2) all Copepoda (*Aglaodiaptomus clavipes*, *Acanthocyclops*, *Mesocyclops edax*, *Tropocyclops prasinus mexicanus*, *Tropocyclops*, *Diacyclops thomasi*, *Diaptomus* spp., calanoid, diaptomid) excluding copepod nauplii and copepodites.

Macrophytes and Filamentous Algae

We assessed lake-wide changes in macrophyte abundance from lake-wide macrophyte surveys conducted by the Wisconsin Department of Natural Resources (WDNR) using a point-intercept sampling grid at 50-m increments for all surveys, except 2005 when the grid was 100 m. Macrophyte surveys were conducted most years during the month of July from 2005–2023 (no survey occurred in years 2006, 2016, and 2018), with a weighted, double-headed garden rake mounted to a pole. The rake was lowered until resting on the bottom, then twisted twice and pulled straight out of the water (Hauxwell and others 2010). All plants recovered from the rake were identified to species and given a rake fullness rating by species of 1 (few), 2 (moderate), or 3 (abundant) to estimate relative abundance. Sites that were labeled “non-navigable (plants)” were also given a rating of 3. In addition, total coverage of plants on the rake was assigned a rake fullness rating (Hauxwell and others 2010). Filamentous algae were not included in the total rake fullness. Maximum depth of macrophyte colonization was obtained from annual WDNR surveys. WDNR point-intercept data were also used to create a bathymetric map of Lake Wingra by averaging depths over all survey years. Bathymetry was estimated to 0.5 m contours and used for spatial averaging.

To evaluate changes in biomass and species composition over a longer time series, we used NTL-LTER macrophyte transect data, which were collected once every summer between late June and early August from 1995 to 2024 on Lake Wingra. Five transects (transects 2, 5, 7, 9, and 11,

Figure S2) running perpendicular to the lake shoreline at consistent locations around the perimeter of the lake were sampled from a boat at depths from 1.0 m to depth of maximum colonization at 0.5-m intervals. At each transect and depth, a weighted, double-headed rake attached by rope was cast off the front left, front right, rear left, and rear right off the boat (total $n = 4$) and dragged 2 m along the bottom and pulled straight out of the water (Deppe and Lathrop 1993). All plants on the rake were identified to species and assigned a density rating ranging from 0 (not present) to 5 (very abundant) based on the extent of coverage on the rake head (Magnuson and others 2022b). The abundance of filamentous algae was also ranked 0 to 5. For each rake cast, water was squeezed from the plants and filamentous algae and weights were recorded using field scales on the boat. Macrophyte and filamentous algal biomass were averaged within three depth intervals (1–1.5, 2–2.5, and 3–3.5 m) across the five transects. A bathymetrically weighted mean rake biomass was then calculated across the depth intervals (Magnuson and others 2022a).

From the NTL-LTER transect data, we calculated relative frequency (%) of each macrophyte species (≤ 2.5 m) to assess changes in species composition in the shallow littoral area. We also compared changes in occurrence to historical data collected in 1969–1970 (Nichols and Mori 1971) and 1991–1992 (Trebitz and others 1993). Macrophytes with 2.5% or less relative frequency throughout the time series were categorized as other. The Shannon-Wiener diversity index (H') was calculated to assess the diversity of species at the lake level accounting for both richness and evenness, using the formula $H' = -\sum(p_i \ln p_i)$, where p_i represents the proportion of each species relative to the total number of species observed.

Remote Sensing

To supplement Secchi and chlorophyll *a* datasets, we used Google Earth Engine to analyze Landsat 7 surface reflectance imagery (USGS Level 2, Collection 2, Tier 1) over Lake Wingra from June to September 1999–2023, filtered to <30% cloud cover and high image quality. Images were clipped to a buffered region around the lake and processed to apply standard radiometric scaling, remove saturated pixels, and mask clouds using the pixel_qa band. A normalized difference index (Red - Blue)/(Red + Blue) was calculated for each image to estimate surface optical properties related to color and water clarity (Chipman and others 2004). The

resulting RBindex time series was averaged across the lake surface area, where a higher RBindex indicates greater turbidity.

Statistical Analyses

Abrupt Shift

Data were analyzed either as raw timeseries or as summer means. All statistical tests and visualizations were performed using R Statistical Software (v4.2.1; (R Core Team 2024)). To detect abrupt temporal change points in the raw summer time series of water quality parameters and RBindex, macrophyte colonization depth, and filamentous algae, we used Pettitt's test (Pettitt 1979), with the *pettit* function from the *trends* package in R 4.2.1. Pettitt's test is nonparametric, rank-based test that identifies a single change point in the central tendency of a time series. We considered breakpoints significant if the test returned a p value < 0.05 .

To compare our response variables pre (< 2008) and post (≥ 2008) the winter 2008 carp removal, we first checked for temporal autocorrelation of summer means using the *acf* function, normality using the *shapiro.test* function, and equal variance using the *var.test* function in base R stats package. Secchi depth, TN, TP, RBindex, and macrophyte biomass all had significant autocorrelation. To assess differences in summer means while accounting for temporal autocorrelation, we employed a Generalized Least Squares (GLS) regression model, with group (pre vs. post 2008) as a fixed effect and an autoregressive correlation structure of order 1 (AR(1)) to account for temporal dependence among residuals. The model was implemented using the *gls* function from the *nlme* package in R. Residual autocorrelation plots were used to assess the AR(1) structure in accounting for temporal autocorrelation. For all other response variables (chlorophyll a, TPM, filamentous algae biomass), we used a GLS model without correlation structure.

Assessing Long-Term Persistence

To test our expectation that nutrient concentrations would become more strongly influenced by external processes post-carp removal (Table 1), we retrieved precipitation data (rain + snow) from the University of Wisconsin–Arboretum meteorological station located in the watershed (43.041, -89.429), USC00470273. Knowing that in this region wet years are associated with higher nutrient delivery and poor summer water quality (Carpenter and others 2018), we calculated precipitation for each year as the sum of daily totals from January

through August. We used linear regression models to test the relationship between precipitation and summer mean response variables (Secchi, nutrient concentrations, chlorophyll a, TPM) before and after carp removal.

Structural Equation Modeling (SEM)

We used structural equation modeling (SEM) to evaluate hypothesized causal relationships among precipitation, nutrient dynamics, and biological responses in Lake Wingra post-carp removal. The model was constructed and fit using the *lavaan* R package (v.0.6-16), with model visualization conducted using the *semPlot* package.

The SEM was developed to explore how precipitation influences mean summer ecosystem state. The model included the following directed relationships: (1) Precipitation was specified as a predictor of TP and Secchi depth. (2) TP (or TN substituted) was modeled to directly influence chlorophyll a and filamentous algae, representing bottom-up nutrient effects. Secchi depth was hypothesized to influence chlorophyll a, filamentous algae, and *Daphnia* abundance (*Daphnia*) through light availability. *Daphnia*, representing large-bodied zooplankton grazers, was further modeled to influence chlorophyll a and filamentous algae, capturing potential top-down control mechanisms. All variables were treated as observed (manifest) variables, and no latent constructs were included. Standardized estimates were extracted from the model and represent the change in the outcome variable associated with a one standard deviation increase in the predictor variable, controlling for other variables in the model.

RESULTS

Response of Carp Removal

We detected an abrupt change in water clarity coincident with the carp removal (Table 2). Pettitt's test identified statistically significant change points ($p < 0.01$) between the summer of 2007 and 2008 in Secchi depth and remotely sensed surface reflectance (RBindex) of the lake and within the summer of 2008 for TN and TP concentrations. Significant breakpoints were found between 2010 and 2011 for macrophyte colonization depth, 2009 and 2010 for macrophyte biomass, and 2007 and 2008 for filamentous algae wet biomass.

GLS models revealed significant changes in Lake Wingra ecosystem state following the carp removal in 2008 (Table 2). Secchi depth significantly increased ($p < 0.01$), with the summer median

Table 2. Summary of Breakpoints and Model-estimated Changes in Ecological Response Variables Before (<2008) and After ($\geq$ 2008) Carp Removal

Response variable	Breakpoint	p value	Model type	Change	p value
Secchi depth (m)	Aug 21, 2007/June 11, 2008	< 0.01	GLS + AR(1)	Positive	< 0.01
Total nitrogen ($\mu\text{g/L}$)	June 11, 2008/June 25, 2008	< 0.01	GLS + AR(1)	Negative	< 0.01
Total phosphorus ($\mu\text{g/L}$)	June 11, 2008/July 9, 2008	< 0.01	GLS + AR(1)	Negative	< 0.01
Chlorophyll a ($\mu\text{g/L}$)	Aug 19, 2019/June 8, 2020	< 0.01	GLS	NS	0.08
Total particulate matter (mg/L)	Aug 9, 2006/Aug 22, 2006	< 0.01	GLS	Negative	< 0.01
RBIndex	July 1, 2007/June 1, 2008	< 0.01	GLS + AR(1)	Negative	< 0.01
Macrophyte biomass (g wet weight)	2009/2010	< 0.01	GLS + AR(1)	Positive	< 0.01
Filamentous algae biomass (g wet weight)	2007/2008	< 0.01	GLS	Positive	< 0.01

Breakpoints in timeseries were identified using Pettitt's test, with p values are reported. Generalized least squares (GLS) models (with an AR(1) correlation structure when temporal autocorrelation was present) were used to identify the direction and significance of response variable change before and after ($\geq$) 2008.

increasing from 0.7 to 1.2 m post-removal (Figure 1j). This corresponds to an increase in photic zone depth from 2.3 m to 3.96 m. TN and TP concentrations declined significantly, with the summer median changing from 956 to 728 $\mu\text{g L}^{-1}$ and 50 to 33 $\mu\text{g L}^{-1}$, respectively (Figure 1k,l). Chlorophyll a had non-significant decline in concentrations, with summer medians decreasing from 20 to 17 $\mu\text{g L}^{-1}$ (Figure 1m); however, TPM median significantly decreased from 4.44 mg L^{-1} to 2.21 mg L^{-1} (Figure 1n). RBindex of the lake surface significantly decreased from a median of 0.08 to 0.014 (Figure 1o). Macrophyte biomass increased significantly from a median wet mass per rake of 264 g to 859 g (Figure 1p). Likewise, filamentous algae biomass increased significantly from 0.08 g wet mass per rake to 34 g (Figure 1q).

Macrophytes expanded as photic zone depth increased (Figure 2). The maximum colonization depth of macrophytes increased from 2.6 m in 2005 to the lake maximum of 3.96 m in 2011 (Figures 1g, 2a). Macrophyte establishment > 3 m was possible post-carp removal due to high water clarity (Secchi > 2) especially in the spring (Figure S3). Spatial coverage of macrophytes continued to increase during the post-removal window. The percentage of grid points sampled that had macrophytes increased from 52% in 2005, to 77% in 2013, and 93% in 2023. Additionally, three times as many locations had rake fullness ratings of "3" (maximum fullness) in 2023 (16 years post biomanipulation) compared to 2013 (6 years post) (Figure 2c,d).

Persistence of New Ecosystem State

Following carp removal, the variability in the annual summer mean TN, TP, and chlorophyll a concentrations was associated with year to year

differences in precipitation (Figure 3; Table 3). In the post-removal period, TP had a strong positive relationship with precipitation ($p < 0.01$, $R^2 = 0.73$), followed by TN ($p < 0.01$; $R^2 = 0.64$), and chlorophyll a ($p < 0.01$, $R^2 = 0.37$). Secchi depth had a negative relationship with precipitation ($R^2 = 0.18$), but was not significant ($p = 0.09$). In contrast, none of the water quality variables showed significant associations with precipitation in the pre-removal period. Both before and after carp removal, TP and TN had positive significant relationships to chlorophyll a concentrations, but the strength of the relationship decreased following the carp removal (Figure 4).

Following the carp removal, *Myriophyllum spicatum* (Eurasian watermilfoil–EWM) and *Ceratophyllum demersum* (coontail) both expanded into previously unvegetated areas. In the DNR surveys, EWM was present at 56% of littoral points before removal, and after removal, peaked in 2012 at 76% of points after removal. The extent of EWM remained high between 2008 and 2015 and then declined in 2016 before expanding again in 2020–2023. Coontail was present at 35% of points before removal and peaked in 2023 at 85% of points. Coontail has consistently exceeded EWM in its frequency of occurrence since 2016. The Shannon-Wiener diversity index showed species diversity in the littoral zone was similar over the long term regardless of carp removal (Table S2).

With expanded habitat availability, filamentous algae biomass significantly increased post-carp removal, but was variable across post-removal years (Figure 1i). The minimum and maximum spatially averaged wet mass ranged from 866 g to 2072 g with a standard deviation of 345 g. Filamentous algae presence was also spatially variable, with

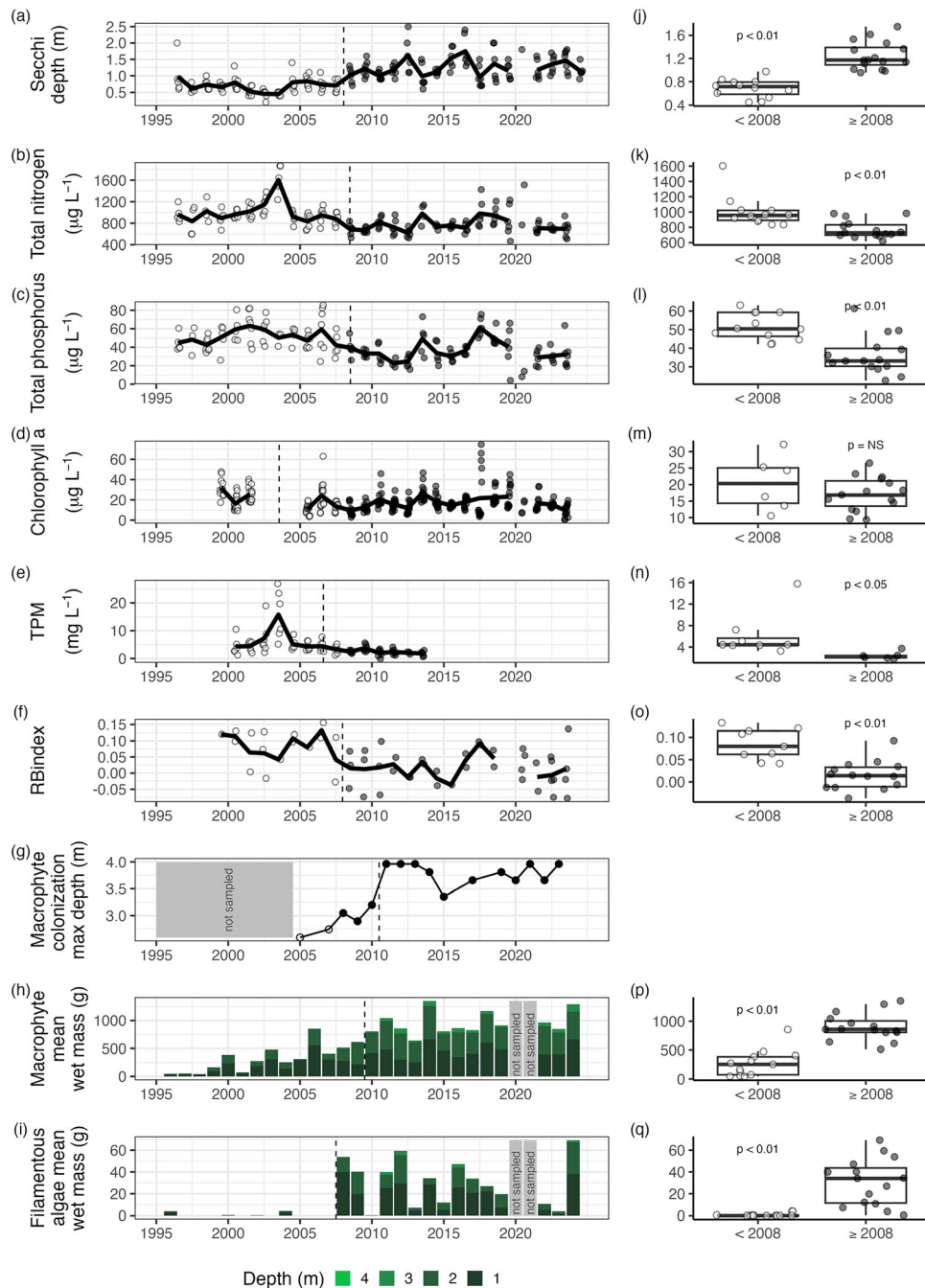


Figure 1. Time series of June–Aug response variables (a) Secchi depth, (b) total nitrogen (TN), (c) total phosphorus (TP), (d) chlorophyll a, (e) total particulate matter (TPM), (f) RBindex from Landsat 7, and (g) max colonization depth of macrophytes, with pre-removal years in white and post-removal in black. The black line represents the summer mean, where 2020 has been removed due to lack of representative data. (h) Area weighted mean wet mass of macrophytes (1–4 m depth), and (i) filamentous algae. Dashed vertical lines in plots (a–i) represent statistically significant breakpoints. (j–q) Boxplots of all summer means grouped by pre-removal (white) and post-removal (black). P values denote significant change in generalized least square model (GLS) before and after ($\geq$) 2008.

higher densities on the western end near where most of the major urban storm sewer outfalls were located. Summer *Daphnia* and Copepoda densities were positively ($p > 0.05$) related to filamentous

algae wet mass in the years after the removal (Figure 5a), while chlorophyll a concentrations were negatively related ($p > 0.05$, Figure 5b).

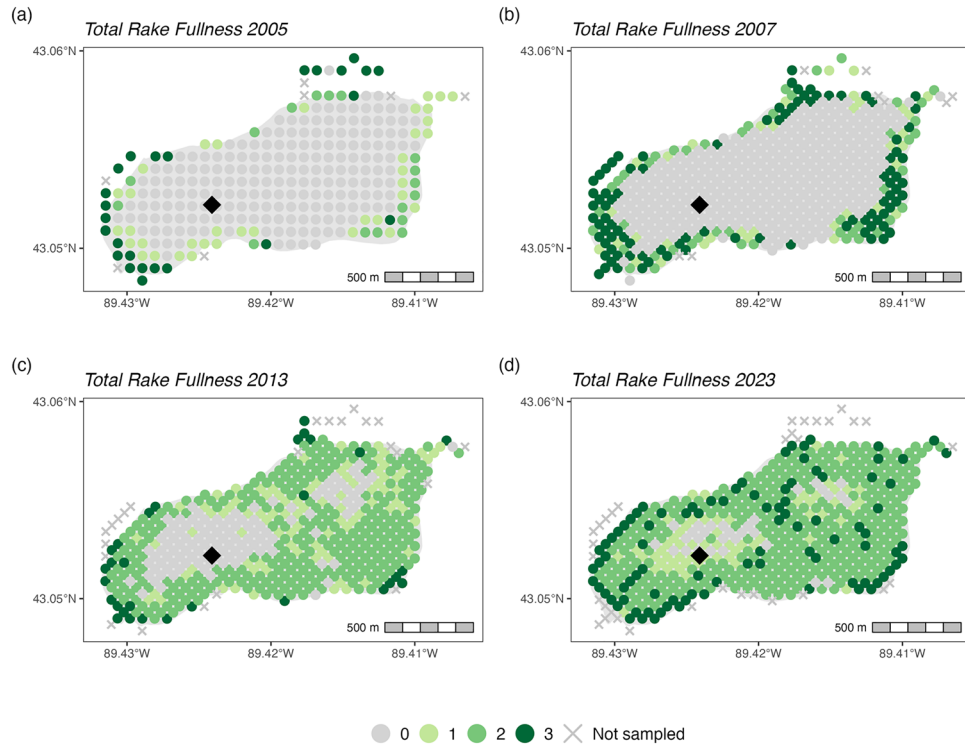


Figure 2. Macrophyte abundance based on rake fullness from WDNR point-intercept surveys for representative years pre-removal in (a) 2005 and (b) 2007 and post-removal in (c) 2013 and (d) 2023. The darker the green, the higher the rake fullness. X marks points that were not sampled. The black diamond represents the NTL-LTER water quality sampling location.

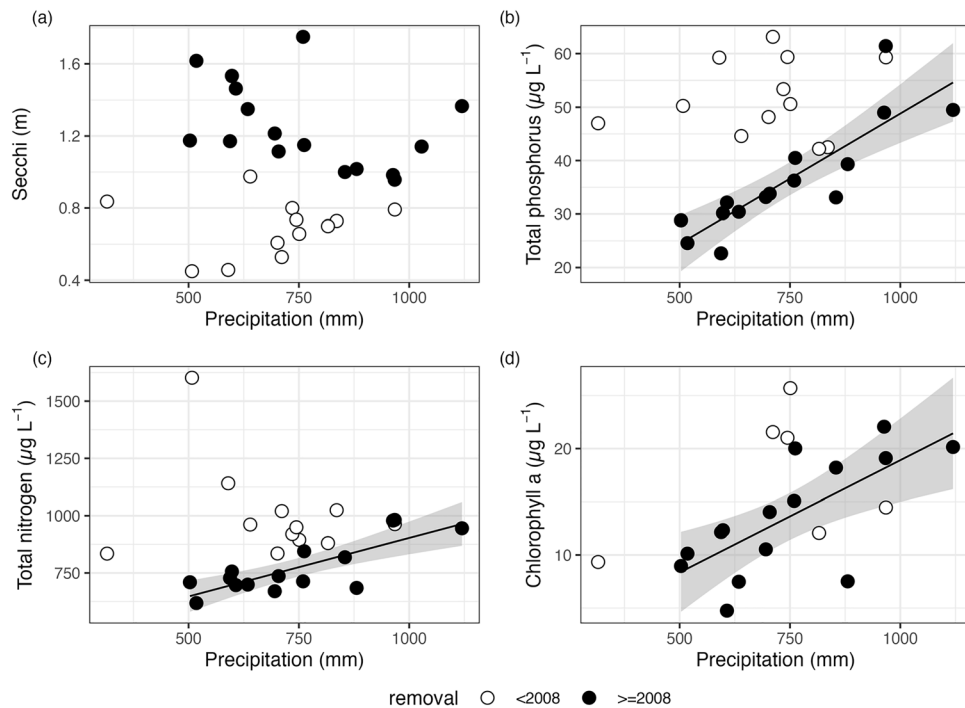


Figure 3. Relationship between total precipitation (January to August) and summer mean of water quality variables (a) Secchi depth, (b) total phosphorus, (c) total nitrogen, and (d) chlorophyll a. Fitted linear regression models are shown when significant ($p < 0.05$).

Table 3. Linear Model Results Evaluating the Relationship Between Summer Median Water Quality Variables and Antecedent Precipitation (January–August) Before and After Common Carp Removal

Response variable	Period	R^2	p value
Secchi depth (m)	Pre	0.014	NS
	Post	0.18	NS
Total Nitrogen ($\mu\text{g/L}$)	Pre	0.06	NS
	Post	0.64	< 0.01
Total Phosphorus ($\mu\text{g/L}$)	Pre	0.019	NS
	Post	0.73	< 0.01
Chlorophyll a ($\mu\text{g/L}$)	Pre	0.095	NS
	Post	0.37	< 0.05
TPM (mg/L)	Pre	0.153	NS
	Post	0.0658	NS

Models were fit separately for each removal period and response variable. Reported values include R^2 and p values for each model. NS = not significant ($p > 0.05$).

For the post-removal ecosystem state, the SEM revealed significant correlations between precipitation, nutrients, and biological responses (Figure 5c). While we are showing results for TP, an SEM built with TN showed similar results (Figure S2). Precipitation was strongly and positively associated with TP (standardized estimate = 0.98), and TP was moderately correlated with chlorophyll a (0.54). Precipitation had a negative relationship with water clarity, as measured by Secchi depth (−0.53). Secchi depth had a strong positive relationship with *Daphnia* density (0.58). Additionally, filamentous algae wet mass was positively correlated with *Daphnia* density (0.51) and negatively correlated with chlorophyll a (−0.41). Several hypoth-

esized relationships, including the direct effects of TP on filamentous algae and *Daphnia*, were negligible and not statistically supported.

DISCUSSION

Abrupt Shift in Lake Ecosystem State Following Biomanipulation

We found that the biomanipulation in Lake Wingra led to an abrupt shift from a turbid state to a macrophyte-dominated clear-water state. In the summer immediately following the carp removal, water clarity increased, nutrient concentrations decreased, and the turbidity of the lake as measured by surface reflectance (RIndex) decreased. Within a few years of new benthic habitat availability, macrophytes had expanded and colonized to new depths, and filamentous algae appeared more regularly, benefiting from the structure provided by the macrophytes.

Before 2008, carp generated strong positive feedbacks that maintained a turbid state in Lake Wingra. Carp bioturbation resuspended sediments and reduced water clarity, inhibiting submerged aquatic vegetation that would otherwise stabilize sediments and improve water clarity. Carp removal disrupted the feedback loop maintaining the turbid state by reducing sediment resuspension (as evidenced by decreased TPM concentrations) and rapidly improved water clarity. With higher water clarity, down to approximately 4 m, the littoral zone in Lake Wingra quickly expanded. Relieved of light limitation (Vadeboncoeur and others 2008), macrophyte colonization by EWM and coontail reached the maximum lake depth within four years (Figure 2), while more sessile and rooted native

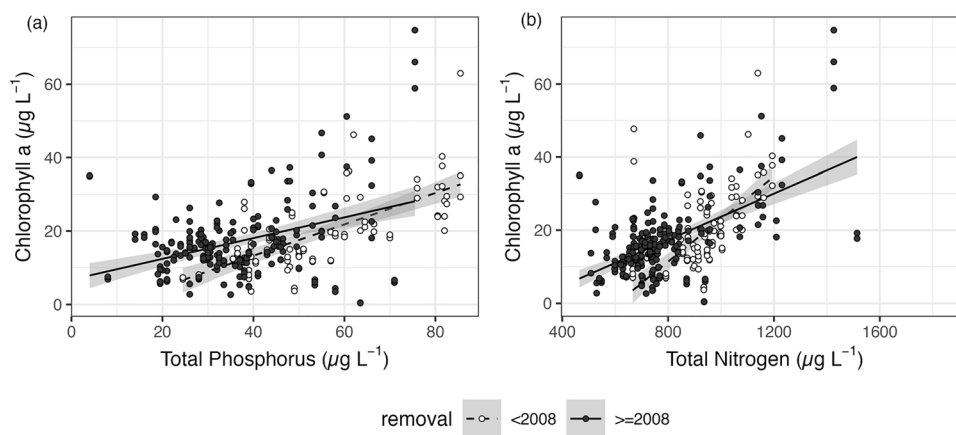


Figure 4. Relationship between chlorophyll a concentrations and (a) total phosphorus ($R^2 = 0.56 < 2008$, $R^2 = 0.16 \geq 2008$) and (b) total nitrogen concentrations ($R^2 = 0.58 < 2008$, $R^2 = 0.35 \geq 2008$) between June and August. Fitted linear regression models are significant ($p < 0.05$).

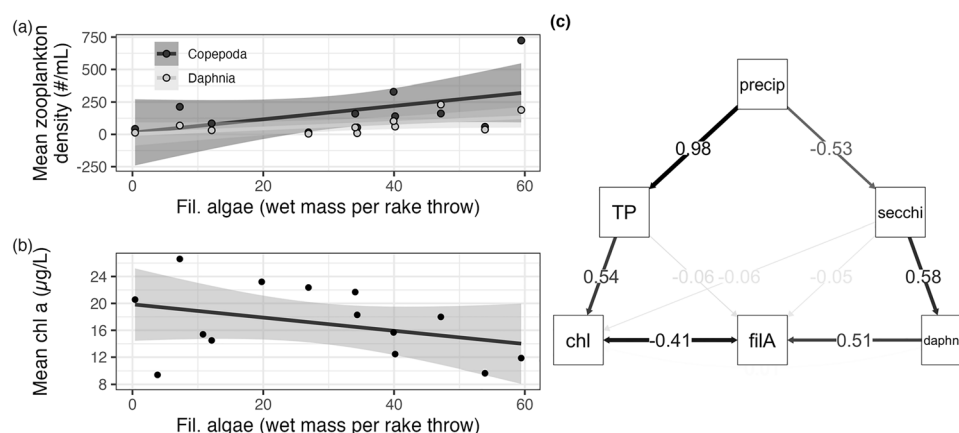


Figure 5. Post-carp removal (≥ 2008) state of Lake Wingra. Relationship between post-removal (≥ 2008) filamentous algae wet mass per rake throw and (a) summer *Daphnia* and *Copepoda* density (p value > 0.05) and (b) mean summer chlorophyll a concentrations (p value > 0.05). (c) Path diagram of structural equation model (SEM) showing standardized estimates between nodes (precip = annual precipitation Jan–Aug, TP = summer mean total phosphorus concentration, secchi = mean summer Secchi depth, chl = mean summer chlorophyll a concentration, filA = filamentous algae wet weight, daphnia = summer mean *Daphnia* density).

species did not greatly expand their coverage. Even without total eradication, a large reduction in carp density can change their feeding behavior. Low abundance reduces competition, resulting in more satiated carp (Zambrano and others 2001). Lin and Wu (2013) examined changes in benthic sediment structure in Lake Wingra and found that one year after the carp removal the originally fluffy and loose sediment layer in unvegetated areas had become more consolidated and stable and drastically less prone to remobilization and resuspension during windy days.

Pelagic chlorophyll a was the only water quality parameter that showed no significant change following carp removal, despite the increase in water clarity attributable to reduced non-phytoplankton particle concentrations. Although we cannot assess changes in zooplankton density, we had hypothesized that herbivorous zooplankton may have increased and contributed to a reduction in chlorophyll a through grazing (Meijer and others 1990; Schrage and Downing 2004). Carp in early life stages (< 100 mm) are known to primarily feed on zooplankton (Sibbing 1988; Meijer and others 1990; Britton and others 2007; Huser and Bartels 2015), while suspended sediments can inhibit the ingestion of phytoplankton by large-bodied zooplankton (Kirk 1991; Kirk and Gilbert 1990). The removal of carp should theoretically reduce zooplanktivory. Even if the effect was brief, as demonstrated by low chlorophyll a concentrations in 2008, increased grazing may have initiated the positive feedback loop sustaining clear-water con-

ditions and enabled macrophyte expansion to further reinforce the feedbacks on water clarity (Lampert and others 1986; Gulati and others 1990).

Persistence of New Ecosystem State

Unlike other lakes which reverted to a turbid state following management interventions, Lake Wingra has persisted in the macrophyte-dominated state for 17 years. We believe this stability is driven by feedbacks between recovering macrophytes and top-down food web pressures that together suppress conditions favoring turbidity and sustain the macrophyte-dominated state.

It has been shown that macrophyte recovery is a key factor in sustaining the effects of biomanipulations (Carpenter and Lodge 1986; Jeppesen and others 1990; Van Donk and others 1993; Benndorf and others 2002; Mehner and others 2002). In Lake Wingra, there was rapid dispersal of nutrient-tolerant submerged macrophyte species, such as *Myriophyllum spicatum* (Eurasian watermilfoil; EWM) and *Ceratophyllum demersum* (coontail). We did not see an increase in species richness in the littoral area (similar Shannon diversity index since the early 1990 s) because of the rapid expansion of EWM and coontail. EWM, an invasive species, has dominated the macrophyte community since its establishment and proliferation in the early 1960s in Lake Wingra (Lathrop and others 2013). EWM is a rooted macrophyte that can take up P from sediments (Smith and Barko 1990). It is tolerant of high nutrient levels and grows quickly by vegetative fragments, allowing it to establish dense pop-

ulations and even persist under turbid conditions (Nichols and Shaw 1986; Lacoul and Freedman 2006; Penning and others 2008) and under the presence of abundant carp populations (Drenner and others 1997, 1998; Chumchal and others 2005). EWM starts growing much earlier in the spring compared to native plants and creates canopy that shades macrophytes of smaller stature (Titus and Adams 1979; Smith and Barko 1990). In contrast, coontail, a native macrophyte, is non-rooted and therefore can expand quickly into deeper habitats and use nutrients in the water column. Similar to EWM, it can also persist in lakes with high P concentrations ($> 0.03 \text{ mg P L}^{-1}$, (Mjelde and Faafeng 1997)). Functionally, both species are similar in that they can develop quickly and form dense canopies, giving them a competitive advantage for light and are superior competitors for nutrients compared to phytoplankton (Kufel and Ozimek 1994). Both species also have high allelopathic potential, which could further inhibit phytoplankton growth and stabilize higher water clarity (van Donk and van de Bund 2002; Hilt 2006).

Lake Wingra is a mesotrophic to eutrophic lake, and the presence of three groups of primary producers (phytoplankton, filamentous algae, and macrophytes) competing for resources (nutrients and light) makes community composition a key factor in the feedbacks maintaining or shifting a macrophyte-dominated state. Filamentous algae can outcompete phytoplankton for water column nutrients (Hansel-Welch and others 2003; Irfanullah and Moss 2005; Trochine and others 2011), and regulate P release from sediments (Genkai-Kato and others 2012), and could be an additional mechanism for persistence of water clarity without measures to reduce external nutrient loading. Filamentous algae appeared in Lake Wingra coincident with carp removal, although its presence varied among subsequent years. The only documentation of filamentous algae prior to NTL-LTER monitoring was in the early 1970s when the dense mats of algae were also concentrated overtop EWM canopies, and on the west end, where nutrient-rich stormwater runoff drains into the lake (McCracken and others 1974; Jones and others 1983). In summers with more filamentous algae, we also measured higher zooplankton densities and lower concentrations of chlorophyll *a* in the water column (Figure 5a,b), although neither of these linear relationships was significant. Increased grazing on phytoplankton may reduce competition for nutrients with filamentous algae, while EWM and coontail provide substrate for more extensive

floating mats of algae, giving it a competitive advantage for light over phytoplankton (Scheffer and others 2012).

At the same time, mats of filamentous algae depend on macrophytes for substrate (Phillips and others 1978; Zhang and others 2020) and can inhibit rooted plant development by shading (Phillips and others 1978; Jones and others 2002; Hansel-Welch and others 2003). Studies have shown that the combined influence of periphyton shading and herbivory can lead to the collapse of submerged macrophytes (Hidding and others 2016; Phillips and others 1978). From our 17 years of monitoring, there is no indication that filamentous algal growth has negatively affected macrophyte biomass.

Although unsubstantiated, we hypothesize that top-down predation of juvenile carp and carp eggs by native fishes such as bluegill is also an important mechanism for maintaining the clear-water persistence (Bajer and others 2012; Poole and Bajer 2019; Vander Zanden and others 2024). Bluegill also predate on macroinvertebrates, which graze on macrophytes Baumann and Kitchell (1974). When comparing Lake Wingra to Danish lakes that underwent removal of $> 200 \text{ kg fish ha}^{-1}$ of planktivorous and benthivorous fish, the Danish lakes returned to pre-restoration conditions after 6–10 years. This was a result of consistent nutrient loading and rebound of some fish stocks (Søndergaard and others 2008). In contrast, carp have not rebounded in Lake Wingra, which we believe is in part due to sufficient top-down food web pressure from centrarchid fish populations.

We do not have sufficient evidence to determine whether the abrupt shift from the turbid to macrophyte-dominated state in Lake Wingra represents a critical transition characterized by alternative stable states. Demonstrating alternative stable states requires showing distinct persistent states, self-reinforcing feedbacks, and hysteresis, where the same external conditions can support different ecosystem states (Kéfi et al. 2016). What we have documented is an abrupt change (Ratajczak and others 2018) associated with shifts in feedbacks that maintained the turbid and macrophyte-dominated states. The abrupt ecosystem change induced by the carp removal may reflect a discontinuous transition between alternative stable states driven by strong feedbacks, or alternatively, a continuous, abrupt transition mediated by weaker feedbacks. Although alternative stable states have been observed in other shallow lakes (Scheffer and others 1993), we do not definitively establish their presence in this study.

Managing for Long-Term Resilience

Manipulating food webs can be a powerful management tool for driving ecosystem changes, but their long-term effectiveness also depends on complex interactions and external pressures. While a desired shift may occur, surprises can arise, and the new state may not be stable if external pressures persist and the feedbacks that maintain that state are insufficient to absorb the variability in internal processes and external drivers (Holling 1973; Hilt and others 2018). For example, in Virginia, large-scale eelgrass reintroduction established self-stabilizing feedbacks, similar to those of freshwater macrophytes, that maintained the state change (Orth and others 2020). However, in the adjacent Chesapeake Bay, the ecosystem reverted to its pre-vegetated state largely due to higher nutrient inputs from the surrounding watershed in conjunction with warming temperature (Lefcheck and others 2017; Orth and others 2020). Food web manipulations, alongside modeling and long-term monitoring (King and others 2023), help reveal the mechanisms that drive the stability of an ecosystem state following an abrupt shift.

One concern is that anthropogenic climate change in conjunction with other drivers (for example, land cover and nutrient transport) is increasing the likelihood of abrupt change across ecosystems (Steffen and others 2015; Ratajczak and others 2018; Turner and others 2020; Jaiswal and others 2021). These dynamics pose a key challenge for the persistence of the macrophyte-dominated state in shallow lakes (Jeppesen and others 2014; Abell and others 2022; Meerhoff and others 2022). The carp removal changed Lake Wingra from a system where nutrient cycling was driven by internal processes, to a system where external nutrient loading driven by precipitation is now the major driver of inter-annual variability in water quality (Figure 5c, S4).

The north temperate region of the USA is projected to receive more total precipitation (Knutti and Sedláček 2013) and more episodic and intense precipitation events that will increase external nutrient loading, especially in urbanized areas with high percentage of impervious surfaces (Moss 2011; Thompson and others 2013). Extreme precipitation events could weaken or overcome the resilience of the macrophyte-dominated state by intensifying external nutrient fluxes, leading to elevated chlorophyll *a* and decreased transparency. In some years, summer TP concentrations in Lake Wingra exceed the threshold of 0.05 mg P L⁻¹, a value identified by Jeppesen and others (2000) as

the upper limit necessary for maintaining a clear-water state in the long term in shallow temperate lakes. As climate change continues to alter disturbance regimes, such as more intense rainfall events, unexpected ecological responses may emerge, making it difficult to anticipate when and where abrupt changes will occur (Turner and Seidl 2023). Long-term persistence of the macrophyte-dominated state will thus require management that links in-lake restoration efforts with watershed nutrient mitigation efforts robust to changing climate pressures (Hilt and others 2018).

CONCLUSIONS

Our 29-year dataset from Lake Wingra provides evidence that a single biomanipulation, without other major in-lake or watershed interventions, can result in a sustained shift in ecosystem state in a shallow eutrophic lake. Following a common carp removal, the shift to a clear-water, macrophyte-dominated state has persisted for over 17 years post-removal, well beyond the 5–10-year duration commonly observed in other lakes. This long-term persistence appears to be supported by the synergistic effects of (1) sustained low carp biomass, (2) the rapid colonization and stabilization of submerged macrophytes, and (3) the emergence of filamentous algae as an additional nutrient sink.

However, the benefits of the clear-water state are tempered by the dominance of invasive macrophytes and the proliferation of filamentous algae, which may compromise ecosystem function and limit desired ecological outcomes (Vadeboncoeur and others 2021; Auer and others 2010; Page and others 2022; Hilt and others 2017). While we did not measure benthic algal diversity, there is a concern of the proliferation of toxic cyanobacteria in freshwater lakes (Wood and others 2020). Additionally, as nutrient dynamics become increasingly governed by precipitation-driven loading, the feedbacks maintaining the current state may be vulnerable to future climatic variability, and reduction goals for external nutrient loading should continue to be pursued. Our findings highlight both the potential and the complexity of managing shallow lakes through biomanipulation. Long-term monitoring is essential not only for documenting shifts in ecosystem state, but also for understanding the mechanisms that underpin their persistence.

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DATA AVAILABILITY

North Temperate Lakes Long Term Ecological Research program data are available through the Environmental Data Initiative repository (<https://edirepository.org/>) at the DOIs listed in the references. Reproducible code (R, Google Earth Engine) is available at https://github.com/algorsky/WI_carp. The Wisconsin Department of Natural Resource aquatic plant point-intercept data is available upon request by emailing dnrbaselineaquatic-plants@wisconsin.gov.

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