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Shallow lake management enhanced habitat and attracted waterbirds during fall migration

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Abstract Lake water levels can be managed in shallow lakes in order to improve water quality and promote aquatic vegetation that presumably benefits waterbirds. We aimed to understand whether waterbird abundance and species richness during fall migrations were positively influenced by managed lake water levels at 32 shallow lakes over 10 years. We conducted annual waterbird surveys that counted 6 million birds and repeatedly measured several in-lake habitat variables. Lakes with water level management had lower water depths, greater water quality and clarity, more submerged aquatic vegetation (SAV), and more wild rice (*Zizania palustris* L.) compared to unmanaged lakes. Redundancy analysis and regressions revealed that the waterbird community and several waterbird species were positively correlated to water level management and SAV; however, waterbirds were apparently responding principally to abundant SAV regardless of water depth or management. Two presented case studies of turbid-state lakes also highlighted that water level management rehabilitated lake habitat and waterbird use for a few years. We concluded that water level management can be an effective tool for increasing SAV and migrating waterbirds, but noted that large bird communities can also occur on unmanaged, deeper wetlands with existing SAV coverage of > 80%.

Keywords Clear water state · Turbid state · Submerged aquatic vegetation · Wetland · Water level management · *Zizania palustris*

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Introduction

Shallow lakes are important habitat for a variety of waterbird species during many or all stages of their life cycles (Baldassarre, 2014). Shallow lakes are defined by average depths of $\sim$ 100 cm, maximum depths of

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<400 cm (the approximate threshold beyond which light attenuation prevents plant growth), and minimal thermal stratification throughout the water column (Scheffer, 2004; MNDNR, 2010). Shallow lakes exist in two alternative ecosystem states: either a clear-water state that is characterized by high water clarity and lush macrophytes or a turbid state characterized by planktonic algae, low macrophyte biomass, and turbid water (Moss et al., 1996; Scheffer, 2004). The clear-water state is typically stable over long time periods, but perturbations can trigger a rapid transition to the turbid state (Phillips et al., 2016). Once in the turbid state, managers may intervene using various techniques to push the system back towards the desired clear-water state (Hanson & Butler, 1994a; Meijer et al., 1994; Moss et al., 1996; Hansel-Welch et al., 2003).

Shallow lakes are managed worldwide in order to achieve sustainability of waterbird habitats (Moss et al., 1996; Scheffer, 2004; Jeppesen et al., 2007; MNDNR, 2010). The root causes of lake degradation are often difficult or impossible to address because the lake is embedded in highly modified landscapes and invading common carp (*Cyprinus carpio* Linnaeus, 1758) are persistent, so in-lake management may be warranted. Management focuses on rehabilitating predominately turbid state lakes by shifting towards a clear-water state, despite the expectation of short-lived benefits and the need for ongoing management because of system instability following restoration (Hobbs et al., 2012; Hanson et al., 2016). Management objectives are often basin specific, but broadly management strives to simulate water level fluctuations that have been impaired due to the constraints of altered landscapes. Water levels in shallow lakes are expected to be naturally variable at multiple scales, but landscape changes over the past century have stabilized the water levels of some lakes and adversely affected water clarity and vegetation (Van Geest et al., 2007; McCauley et al., 2015). Therefore, one common management strategy manipulates water levels to increase water quality and aquatic vegetation abundance. Partial and complete lake drawdowns to temporarily or permanently lower water depth can improve water clarity by consolidating nutrients in the sediments (Coveney et al., 2002), promoting abundance of aquatic vegetation (Beklioglu et al. 2006), and increasing wild rice (*Zizania palustris* L.) where lake conditions are appropriate (Moyle, 1944; Pillsbury & McGuire, 2009; Aagaard et al., 2018). Also, the manipulation of fish communities via drawdown is a common strategy to improve wildlife habitat (Hanson & Butler, 1994b; Perrow et al., 1997; MNDNR, 2010). Thus, it is expected that shallow lake management will provide high-quality habitat for waterbirds during migration, although there are only a few, single case studies to date that explicitly link management, habitat change, and waterbird use (Scheffer, 2004).

Lake Christina in Minnesota, USA and Lake Krankesjön in Sweden provide two influential case studies as evidence of shallow lake habitat management influence on waterbird use (Hanson & Butler 1994a, b; Hargeby et al., 1994, 2007; Hansel-Welch et al., 2003; Hansson et al., 2010). In simple summary, both systems were monitored for 20+ years providing a time series of how management had transitioned the lake from a turbid state to a clear-water state and temporarily increased bird use. These two studies showed convincing evidence of concept, yet the scientific literature would benefit from repeatability of these results by examining multiple managed shallow lakes compared to those that are not managed.

Long-term datasets on waterbirds and habitat conditions are uncommon, but provide understanding of how lake management can affect habitat and wildlife. The state of Minnesota in the USA. began surveying shallow lake habitats as early as the 1940 s to furnish wildlife managers with the basic information needed for management. To date, the Minnesota Department of Natural Resources (MNDNR) continues the legacy of shallow lakes habitat and waterbird population surveys (https://www.dnr.state.mn.us/wildlife/shallowlakes/index.html; and https://www.dnr.state.mn.us/hunting/waterfowl/reports.html). At Lake Christina, the two surveys demonstrated the utility of shallow lake management on habitat and bird use (Hanson & Butler, 1994b; Hansel-Welch et al., 2003).

Our objective was to understand how lake habitat and waterbird use compared between managed and unmanaged shallow lakes. We hypothesized shallow lake management that explicitly focused on water level management for enhancing lake water quality and submerged aquatic vegetation (SAV) and wild rice would exceed conditions of unmanaged lakes. We also hypothesized that these high-quality habitat conditions in managed lakes would attract greater densities of waterbirds during fall migration. We conducted a 10-year study on 32 shallow lakes to relate lake management to habitat conditions and waterbird use during fall migration.

Study area

The 32 shallow lakes in Minnesota, USA (data available at (https://doi.org/10.5066/P9QJ1CBR) were historically and currently important for waterbirds. They spanned the entire state and were within three major biomes, including prairies (which were under intensive, row-cropped agriculture), deciduous forests, and boreal forests. These 32 shallow lakes ranged in size from 87 to 3800 hectares (median: 370 hectares). Managed and unmanaged lakes were of similar size (Supplementary Materials F1, available online in Supporting Information). The lakes were either semi-permanent or permanent with an average depth of 140 cm (range 60–280 cm deep). The shallow lakes had ice cover for $\sim$ 5 months of the year, could exhibit fish kills over winter due to anoxia, and occasionally would freeze to the sediments. Our study spanned years 2003–2012 with repeated, annual habitat and waterfowl surveys occurring during this timeframe. Eleven lakes had a designated full or partial migratory waterfowl feeding and resting area (MWFRA) to prevent hunter disturbance during the waterfowl hunting season by providing a zone of the lake with no motorized boat use. Four lakes had a partial MWFRA, seven lakes had a fully designated MWFRA, and 21 lakes had no MWFRA. One lake (Thief) had 40% of the lake in an inviolate refuge with no access during the waterfowl hunting season. The MWFRA status was not considered "management" in our study.

Methods

We polled MNDNR wildlife managers to compile study sites that were known to have historical waterbird migration use and their best records of management activities or lack thereof. Lakes were also selected to represent a range of biomes and to create a balanced design by biome. We were confident in whether a lake was managed or not, but the exact details of management frequency and dates were uncertain except for the two case study lakes presented (Lakes Maria and Christina).

We assigned the selected lakes to two treatment groups: managed or unmanaged, but could not control assignments to treatment. Non-random treatments precluded full confidence that these 32 study sites properly represent the larger population of shallow lakes. The managed lakes were, *on average* across the 10-year study, in relatively poor condition compared to unmanaged lakes (Supplementary Materials F2). In fact, poor habitat condition, such as high nutrients and chlorophyll *a*, were triggers for management. Similarly, lakes in good condition (i.e., low nutrients and chlorophyll *a*) were more likely to be classified within the unmanaged treatment group. Management focused on lakes that needed habitat improvements and not lakes that already had high-quality habitat. This inherent bias of non-random treatment assignment affected the statistical results and inference. In order to find support for our hypothesis that plant abundance and duck use on managed lakes were similar or greater than unmanaged lakes, the magnitude of management effects must be substantial.

The "management" of the lakes explicitly focused on water level management, but varied slightly in management techniques, timing, and frequency. Management activities included either a lake drawdown, rotenone chemical treatment, or beaver removal. All these management actions have the same objectives and outcomes; that is to control water depth, minimize water level fluctuations, and kill fish that degrade lake quality. Most information on lake management was collected through personal communications with lake managers, newspaper reports, and MNDNR records. Of our study lakes, 10 managed lakes had a water control structure that temporarily lowered the water level of the entire lake to induce fish kills. The lakes varied in the season of drawdown, but most occurred in late summer or fall when water levels were naturally low. The refilling of the basin occurred naturally from groundwater or precipitation, and the refilling could occur the following spring or later. The frequency and duration of drawdowns or beaver removal varied, but drawdown occurred at least once during the study period and beaver and dam removal was ongoing in the managed lakes. The wild rice lakes were always managed by beaver and dam removal and never by water control structures. The 16 unmanaged study lakes did not have any management activities prior to or during the study. We randomly selected wild rice lakes ($n = 12$) that were known to have wild rice as a component of the vegetation community (https://resources.gisdata.mn.gov/pub/gdrs/data/pub/us_mn_state_dnr/biota_wild_rice_lakes_dnr_wld/metadata/metadata.html#Identification_Information). We also provided two case studies to show the relations of specific management activities, habitat, and waterbird use through time. In summary, we sampled a total of 32 lakes, 16 of which were managed and 16 lakes that were not. Of these study lakes, 12 were rice lakes ($n = 6$ managed rice lakes, $n = 6$ unmanaged rice lakes).

Sampling waterbirds

We designed aerial waterbird surveys to capture a broad range of taxonomic and functional waterbird guilds during fall migration. Also, our waterfowl surveys were specifically designed to compare the *relative* abundance and densities of birds between our treatment groups and not designed to estimate *actual* or *absolute* abundance or density. Therefore, we report relative abundance and relative density throughout the paper. Density was calculated as follows: count of species / wetland area. Species richness was calculated as the total number of bird species on the lake on each sampling date. All lakes used the same sampling methodology throughout the entire study period.

We conducted repeated aerial waterbird surveys 3–7 times/year on each study lake in the fall for 10 years (2003–2012). We began surveys 1 week prior to the start of the regular migratory waterfowl hunting season (mid-September) and continued until the end of the waterfowl season (late-November) or until the lakes froze. October through November is the principal passage of most migrant waterbirds along the Mississippi flyway, and Mallards (*Anas platyrhynchos* Linnaeus, 1758) will remain in Minnesota as long as food and open water is available (Bellrose & Crompton, 1970; Baldassarre, 2014), so our sampling frame captured peak migration. Hunters can deter bird use on lakes, and so we monitored the lakes repeatedly each fall and during the daytime with closed hunting to reduce uncertainty in our counts. Because we sampled at weekly to bi-weekly intervals and typically only had one observer, we could not calculate waterbird detection rates. The waterbird surveys were conducted an average of 5 times each year on all lakes. We collected count data for 22 species of waterbirds. Because of the variability of waterbird count data, we determined that at least 3 surveys/year was the minimum needed for data analysis. The flights were <150 m and slow with one pilot and one observer doing waterbird counts. The observer attempted a full count of waterbirds on the lake, which was a crude estimation but possible given most lakes were small and our objective was relative abundance.

Shallow lake habitat sampling

We conducted comprehensive lake habitat surveys at least every 3 years during the study. Each field survey collected information on water depth, water chemistry, chlorophyll *a* concentration, and wild rice and SAV frequencies of occurrences. We used the National Wetlands Inventory Cowardin Classification shapefiles to quantify basin area, which was calculated as the sum of open water and emergent vegetation polygons. First, we collected a water sample towards the center of the lake. Water was collected in acid-washed bottles, stored on ice in a cooler, and immediately shipped on ice to the Minnesota Department of Agriculture Laboratory Services for analyses of total phosphorus, chlorophyll *a*, conductivity, and total dissolved solids. We applied the point intercept and line intercept quantification method for determining sampling points for collection of some water parameters and SAV (Madsen, 1999). The entire lake was gridded using ArcMap software and each grid provided a sampling point for water depth, water clarity using a Secchi disk, plants present or absent, and the plant species present at each sample point. Grid size varied by lake size, but sampling points were separated by at least 20 m. The lakes ranged from 35 to 280 points (average: 90 points) because the number of sampling points increased with lake size. The points were uploaded to a Garmin 76 GPS unit for field navigation (3-m resolution). At each point, one circular plant rake (35 cm diameter) was dragged along the bottom of the lake for 180 cm, and we identified each SAV species present on the hook. The individual points were compiled for each lake to determine frequency of occurrence for SAV and wild rice.

Data analyses

We tested for the effects of shallow lake management on habitat variables and waterbird use by conducting three analyses: (1) non-parametric *t*-tests and calculated effect sizes to test the differences in-lake characteristics between treatments, (2) redundancy analysis (RDA) to relate the waterbird assemblages, management, and in-lake habitat variables, and (3) multiple regressions to test waterbird species-specific responses to management and vegetation. We used these differing and complementary techniques to infer biologically significant differences between managed and unmanaged lakes. We report the *p*-value with degrees of freedom, treatment effect size (Cohen, 1977), relative magnitude of differences, and graphic trends. All these analysis outputs and previous literature were used to conclude what constitutes biologically significant results and where uncertainty remains (Wasserstein et al., 2019). We performed statistical analyses using the software R 4.0.5 and 'base' package (R Foundation for Statistical Computing, 2018).

We ran diagnostic tests to ensure that the model assumptions were appropriate for the models. We generated non-biased parameter estimates and transformed the data if necessary. We plotted residuals of each regression model to examine the data distributions, variances, and outliers. The plots of residuals versus fitted values showed that the data fit the model well and there were no concerning variances or outliers. Next, we tested for correlations among our predictor variables because multicollinearity can compromise model fit. The predictor variables that were correlated ($r > 0.4$) included water clarity, water depth, total phosphorus, chlorophyll *a*, and SAV (Supplementary Materials F2).

We preformed Wilcoxon rank sum tests (non-parametric *t*-tests) for each of the lake variables to determine if they differed by treatment. The data required non-parametric testing because the data distributions and variances remained skewed after transformations.

We used waterbird count data from ∼ 60 sampling dates (3–7 flights per fall for 10 years) for the following response variables: "total duck density (all Anatidae members except geese and swans)", "Ring-necked Duck (*Aythya collaris* Donovan, 1809) density", "Mallard (*Anas platyrhynchos*) density", "Coot (*Fulica americana* Gmelin, 1789) density", "Swan (*Cygnus buccinator* Richardson, 1832) density", "Scaup [*Aythya affinis* (Eyton, 1838) and *Aythya marila* (Lineaeus, 1761)] density", and "waterbird species richness." The waterbird response variables were calculated as a maximum *annual–peak count*; specifically, we calculated the annual maximum value for the waterbird surveys (i.e., the maximum value of the 3–7 flights per fall) for every year of the 10-year study period. The measured environmental predictor variables included the following: management (categorical; yes or no), SAV (discrete variable, bounded from 0 to 100% frequency of occurrence), and wild rice (discrete variable, bounded from 0 to 100% frequency of occurrence). We used the maximum annual lake habitat data from 3+ sampling dates (range 3–8 sampled years within the 10-year study period). We chose SAV as the primary predictor variable for habitat quality in the regression modeling because the chlorophyll *a* and SAV were principal drivers of the variation (Supplementary Materials F2) and SAV was an integrated measure of water quality. Wild rice was not strongly correlated with SAV and the variance inflation factors (VIF) found no redundancy in either model (VIF<10), so all predictor variables were included. We expected high variations in the ecological data and considered this in our interpretations.

We conducted a RDA in order to relate waterbird abundance, lake management, and select environmental variables. A RDA is a multivariate extension of multiple regression where the ecological community is constrained by linear combinations of the predictor variables. The waterbird community variables were Chord transformed because this produced the highest amount of variation explained. We conducted a permuted, multivariate analysis of variance (PERMANOVA; perm = 9999) to assess the significance of the overall RDA model, RDA axes, and RDA terms using R's 'vegan' package (Oksanen, 2019).

Lastly, we used multiple linear regression modeling with repeated measures as a complement to the RDA and to examine species-specific responses to the key predictor variables. We ran the same regression model structure for each of the response variables. The model structure was as follows:

$$\text{Waterbird response variable} = \text{management} + \text{SAV} + \text{wild rice} + \text{error (lake/time)}$$

where the *waterbird response variable* was a continuous variable; *management* was either the managed or unmanaged treatment and a binary variable; *SAV* was a discrete variable (bounded from 0 to 100% frequency of occurrence), *wild rice* was a discrete variable (bounded from 0 to 100% frequency of occurrence), and *error* represented unexplained variance (calculated as the ratio of between-subject variance, *lake*, and the within-treatment variance from repeated measures through *time*).

Results

In summary, the lakes that were managed had poor habitat conditions on average, particularly in the first few years of the study. However, examining the annual maximum habitat conditions and waterbird use at managed lakes revealed much greater SAV and wild rice, and marginally greater waterbird counts and species richness, compared to unmanaged lakes (Figs. 1, 2, 3, Table 1). The SAV frequency of occurrence was typically the most informative predictor variable to describe waterbird densities in the various regression models. The graphs, RDA, and regressions concur regarding biologically significant effects of management and SAV on waterbird use of shallow lakes; 20–40% of the variation in relative waterbird densities among the 32 study lakes was explained by these two factors alone (Figs. 2, 3). Two presented case studies showed that management substantially increased SAV the following growing season and waterbird use the subsequent fall, but the effects persisted only for 1–5 years.

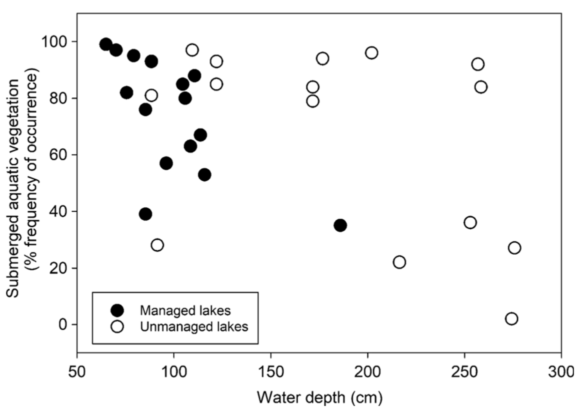

Fig. 1 Lake management created shallow water depths (< 125 cm) and abundant SAV (> 60% frequency of occurrence). The SAV was often greater in shallow water depths, but could also be abundant in unmanaged, deeper lakes with good water clarity

Management influenced in-lake habitat for waterbirds

Managed lakes had similar or greater desired habitat conditions for waterbirds compared to those of unmanaged lakes. Managed lakes had an average water depth of 150 cm, whereas unmanaged lakes had an average water depth of 300 cm ($W(31) = 221.5$, $P < 0.001$; effect size = large; Table 1). Managed lakes tended to have greater SAV and lower chlorophyll *a* (Table 1, effect sizes = large). The SAV was greatest in managed lakes with shallow water depths ($F(2,29) = 3.98$, $P = 0.029$, $r = -0.43$; Fig. 1) and lakes with high water transparency ($F(2,29) = 15.12$, $P < 0.001$, $r = 0.71$).

Of the wild rice lakes ($n = 6$ managed lakes, $n = 6$ unmanaged lakes), the managed rice lakes had 4× greater frequency of occurrence of wild rice than unmanaged lakes ($W(31) = 2$, $P = 0.009$; effect size = very large; Table 1; Fig. 2). Managed lakes averaged 77% frequency of occurrence of wild rice over the entire lake, although several managed lakes neared 100% frequency of occurrence. Wild rice increased with shallower water depths ($r = -0.27$), greater water transparencies ($r = 0.26$), and low total phosphorus concentrations ($r = -0.26$), and these habitat characteristics were often achieved in managed lakes (effect sizes = large, Table 1). Specifically, lakes with > 50% wild rice frequency of occurrence had an average water depth of < 125 cm, water transparency to the bottom of the lake, and total phosphorus concentrations of < 0.05 mg/L–P.

Summary of waterbird surveys

Over the 10-year study, we counted a total of 22 bird species from the aerial surveys. The total bird counts each year varied from 150,000 birds (in year 2008) to 1.4 million birds (in year 2005). We counted a total of 6.1 million waterbirds during the fall migration period over this 10-year study. Waterbird counts and density

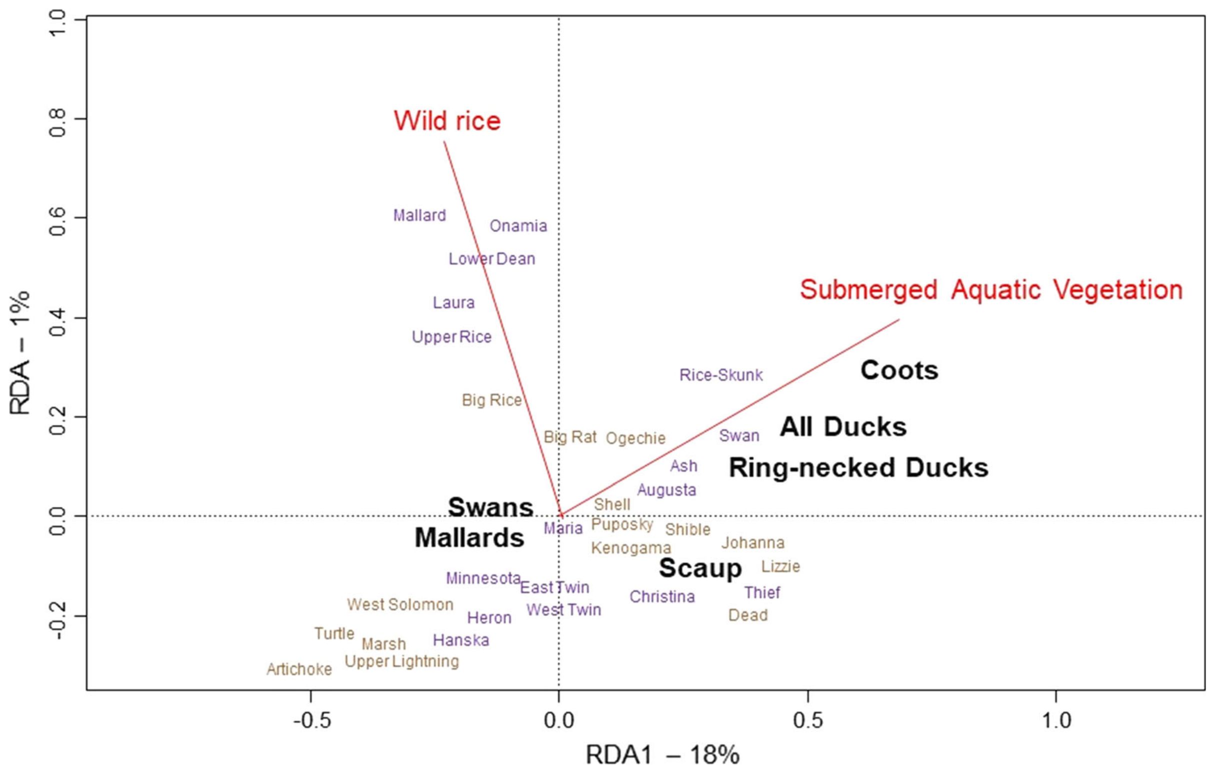

Fig. 2 A multivariate redundancy analysis (RDA) shows the relationships of waterbirds to wild rice (*Zizania palustris*) and submerged aquatic vegetation in managed (violet) and unmanaged (brown) shallow lakes. The densities of the waterbird community (Mallards, Ring-necked Ducks, Swans, Coots, Scaup, and All Ducks) were strongly influenced by submerged aquatic vegetation, but not wild rice or management. Coots, Ring-necked Ducks, and All Ducks (18 duck species combined) were positively associated with submerged aquatic vegetation, but Swans, Mallards, and Scaup were more influenced by factors not measured herein. The managed and unmanaged lakes shared similar waterbird species composition and abundances, as evidenced by the intermixing of sites in ordination space. Although managed lakes had the highest wild rice composition, waterbird densities were not correlated with rice occurrence

were highly variable across the 32 study lakes, among the 3–7 flights per fall, and over the 10 years of study (Supplementary Materials F3). The annual peak densities of ducks across the 32 lakes ranged from 0 to 7 ducks/ha and averaged 0.1 ducks/ha. At a single lake in fall, waterbird counts were often negligible, but then could spike several orders of magnitude within a week. Inter-annual variation was also considerable at most lakes; one example is Lake Maria that had duck densities <1 ducks/ha with a 1-year exception of 7 ducks/ha. Another example showed that Ring-necked Duck maximum annual counts averaged 5000 birds, but were up to 15,000 birds at Lake Christina.

Waterbirds were attracted to high-quality habitats

The multivariate RDA revealed that the densities of the waterbird community members (Mallards, Ring-necked Ducks, All Ducks, Swans, Scaup and Coot) were associated with SAV, but not associated with management or wild rice ($F(2,29) = 3.14$, $P = 0.054$). The RDA Axis 1 ($F(1,29) = 6.27$, $P = 0.042$) and the RDA term, SAV, were key predictors of the waterbird community ($F(1,29) = 4.69$, $P = 0.037$). Coots, Ring-necked Ducks, and all ducks (18 duck species combined) were positively associated with SAV. However, the Swans, Mallards, and Scaup were more influenced by factors not measured herein. The managed and unmanaged lakes shared similar waterbird species composition and densities, as evidenced by the intermixing of sites in ordination space.

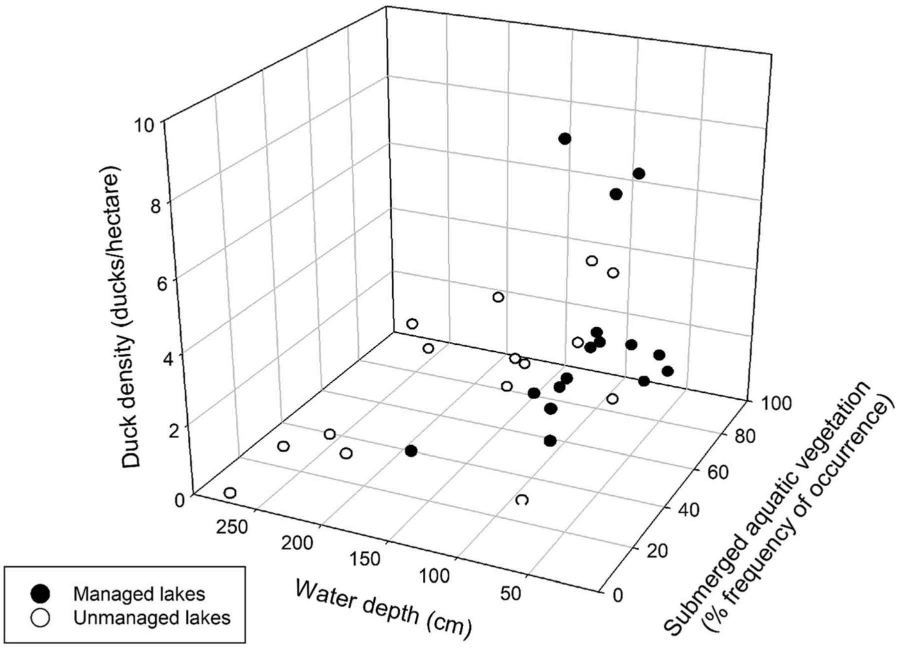

Fig. 3 A 3-dimensional scatterplot highlighting the relations between lake management on water depths, submerged aquatic vegetation (SAV), and duck densities. Annual-peak duck densities were marginally greater on managed lakes which typically had shallow water depths (< 125 cm) and SAV abundance > 60% frequency

Although managed lakes had the highest frequency of wild rice, waterbird densities were not correlated with wild rice.

Regression analysis indicated that the total duck density was positively influenced by management and SAV, but not wild rice ($F(3,28) = 3.02, P = 0.047, r^2 = 0.24$). The total duck density was not predicted by MWFRA status ($F(1,30) = 0.01, P = 0.907, r^2 = 0.01$; Supplementary Materials F4). Management may have marginally increased duck use of shallow lakes ($\beta = 0.16, P = 0.101$), but SAV was the most significant term in the model. The managed lakes tended to have higher SAV and sometimes higher duck density (Figs. 2, 3). Overall, duck densities were typically <2 ducks/ha for managed and unmanaged shallow lakes, but three managed lakes had annual maximum duck densities exceeding 6 ducks/ha (Supplementary Materials F5). Interestingly, the three managed lakes with highest duck densities were small basins that were embedded in a highly row-cropped agricultural landscape and did not have MWFRA status.

We examined a few species-specific responses to management and aquatic plants. Ring-necked Duck density marginally increased with management ($\beta = 0.17, P = 0.075$), but substantially increased with SAV ($\beta = 0.43, P = 0.017$), particularly at SAV frequency of occurrence >80% (Supplementary Materials F6). Conversely, mallard density was not related to management or aquatic plants ($F(3,28) = 0.10, P = 0.958, r^2 = 0.01$) or water depth ($r^2 = 0.07$). Coot density was positively correlated to SAV, but not management or wild rice ($F(3,28) = 3.6, P = 0.026, r^2 = 0.28$). Coots thrived with SAV, especially at frequency of occurrence >75% ($\beta = 0.90, P = 0.011$). Coot densities were typically < 2 Coots/ha, but were as high as 9 Coots/ha. Scaup and Swans had highly variable densities through the 10-year study, and the graphs and models indicated that these waterbirds were not clearly influenced by management, SAV, or wild rice ($P > 0.10$). Swans were moderately associated with shallow water depths ($r^2 = -0.21$). Neither Scaup nor Ring-necked Ducks, which are both diving species, were sensitive to water depth ($r^2 < 0.03$).

Species richness ranged from 0 to 17 waterbird species during any one aerial survey and we detected 22 total species throughout the 10-year study. Species richness was positively correlated with lake size ($r^2 = 0.41$). After accounting for lake size, species

Table 1 The shallow lake characteristics of our study sites ($n = 32$ lakes, sampled 3+ times over a 10-year period)

	Basin size (ha)	Water depth (cm)	Secchi depth (cm)	Total P (mg/L)	Conductivity (umhos)	Total dissolved solids (mg/L)	Chl. *a* (mg/L)	SAV (% frequency of occurrence)	Wild rice (% frequency of occurrence; $n = 6$)
Managed shallow lakes ($n = 16$)	970 (1240)	150 (90)	90 (40)	0.1 (0.05)	474 (283)	326 (241)	0.02 (0.02)	80 (27)	77 (28)
Unmanaged shallow lakes ($n = 16$)	810 (840)	300 (150)	150 (80)	0.2 (0.10)	504 (379)	368 (291)	0.09 (0.11)	62 (34)	22 (21)
Effect size (Cohen's D)	0.2	−1.2	−1.0	−0.2	−0.1	−0.2	−1.0	0.6	2.2
Relative magnitude of differences (Cohen's D)	Small	Large	Large	Small	Small	Small	Large	Moderate–Large	Very Large

We calculated the maximum habitat conditions per lake over the 10-year period and herein report the average-maximum conditions (± 1 standard deviation) by treatment group. Total P = total phosphorus; Chl *a* = chlorophyll *a*; SAV = submerged aquatic vegetation

richness was marginally greater at managed lakes, but not related to SAV ($F(3,28) = 2.6, P = 0.075, r^2 = 0.22$). Species richness averaged to 4 species at unmanaged lakes, but 6 species at managed lakes ($\beta = 0.17, P = 0.063$).

Lake Maria: case study

Lake Maria is a 170-ha shallow lake embedded within a row-cropped, agricultural landscape. Lake Maria continues to be a historically significant waterfowl lake with a long history of stakeholder input regarding lake management. Historical accounts and photos indicated that Lake Maria had abundant SAV and significant waterbird use until the 1970 s when carp invaded, lake water levels stabilized, and water quality declined.

In response, the MNDNR implemented management in 2005–2007. In 2005, they installed a water pump and an electric fish barrier and manually removed 1000+ large common carp. A complete drawdown from spring through fall 2006 removed about 90 cm of water from the lake and left an average water depth of 25 cm by August 2006. A small ditch adjacent to the lake was treated with rotenone over the winter of 2006–2007 and no carp were detected after test netting in spring 2008.

We monitored water quality, SAV, and waterbird data before and after management. By summer 2007 and thereafter, total phosphorus decreased by more than an order of magnitude (concentrations <0.1 mg/L–P), Secchi depth increased threefold, and chlorophyll *a* declined from an average of 0.3 mg/L to 0.001 mg/L. The SAV increased from < 15% frequency of occurrence to ~ 100% frequency of occurrence for 8 years after management. In the fall after management, the total duck density was dominated by Mallards and had increased from < 1 duck/ha to 7 ducks/ha (Fig. 4). However, the duck densities returned to pre-management conditions within 1 year despite the SAV and water quality remaining high for at least 8 years post management.

Lake Christina: case study

Lake Christina is a 16,000-ha shallow lake (average depth: 150 cm) in west-central Minnesota. The lake has a long history of waterbird production, staging and feeding, as well as a long-term ecological monitoring

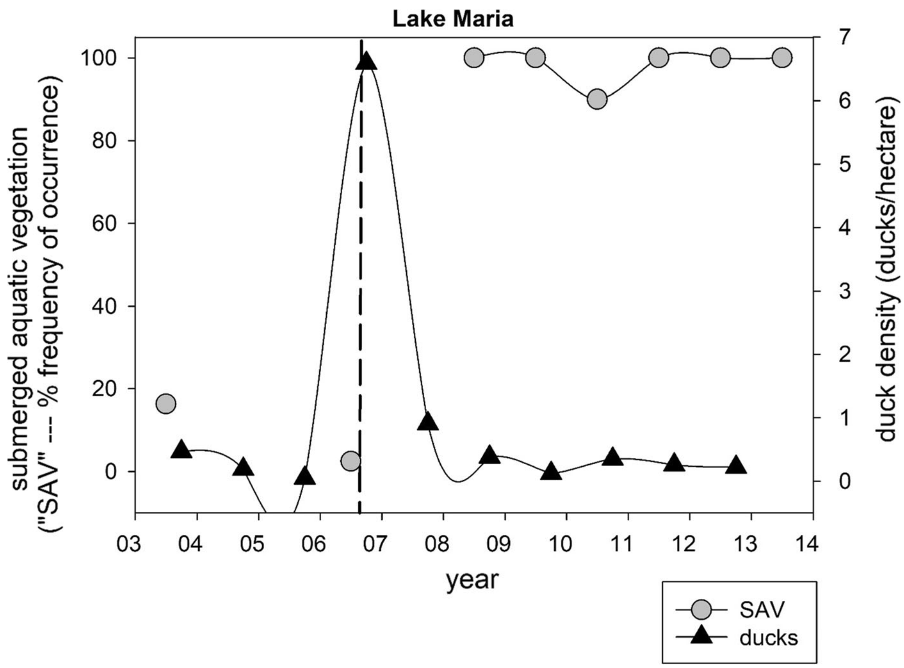

Fig. 4 Lake Maria underwent a managed drawdown and manual carp removal in late summer 2006 (dashed line). The management actions increased submerged aquatic vegetation for 8 years thereafter and increased duck use immediately following the actions, but only persisted for 1 year. Habitat data were not collected in 2004, 2005, and 2007

program. Lake Christina was thought to be in the clear-water state until the early 1960 s when the lake had changed to a turbid state. To return the lake to the clear-water state, several management treatments occurred in the years 1965, 1987, 2003, 2012, and 2018. Following an aerial rotenone treatment in 1987 that induced lake-wide fish kills, Hanson and Butler (1994a, b) documented increased water clarity, reduction of chlorophyll *a*, increased frequency of occurrence of SAV, and increased waterbird relative abundance. Further, the macrophyte community became dominated by *Potamogeton* spp. and *Chara* spp. (Hansel-Welch et al., 2003). The magnitude of results observed at Lake Christina in part helped to justify this research to determine if those results could be repeated at Lake Christina and whether similar results were being realized at other managed shallow lakes.

We documented that management had substantially increased SAV frequency of occurrence, altered plant species composition, and increased duck density. In fall 2003, Lake Christina underwent a rotenone application because the SAV coverage was $< 50\%$ and fall waterbird use was ~ 400 ducks. After treatment, SAV was 100% and most aquatic plants increased in frequency after treatment (Fig. 5), including *Najas* spp., *Potamogeton* spp., *Myriophyllum* spp., *Ruppia maritima* L., *Chara* spp., and *Stuckenia pectinata* (L.) Böerner. Fall duck use had spiked from ~ 400 birds to more than 4000–40,000 waterbirds. At Lake Christina, counts were typically < 2000 Coots most years; however, following rotenone treatment in 2003, the Coot counts were $> 200{,}000$ for four consecutive years. After 2008, SAV and waterbirds declined and resulted in managing with a drawdown in 2012. Again, following management, SAV increased to 100%, but we did not collect waterbird count data.

Discussion

Our rare, long-term dataset that integrated lake habitat and waterbird metrics showed positive outcomes of wetland habitat enhancement on waterbird use during fall migration. Duck density was positively correlated to management, and up to 40% of the variation in waterbird density was explained by lake management and SAV. Management facilitated other important

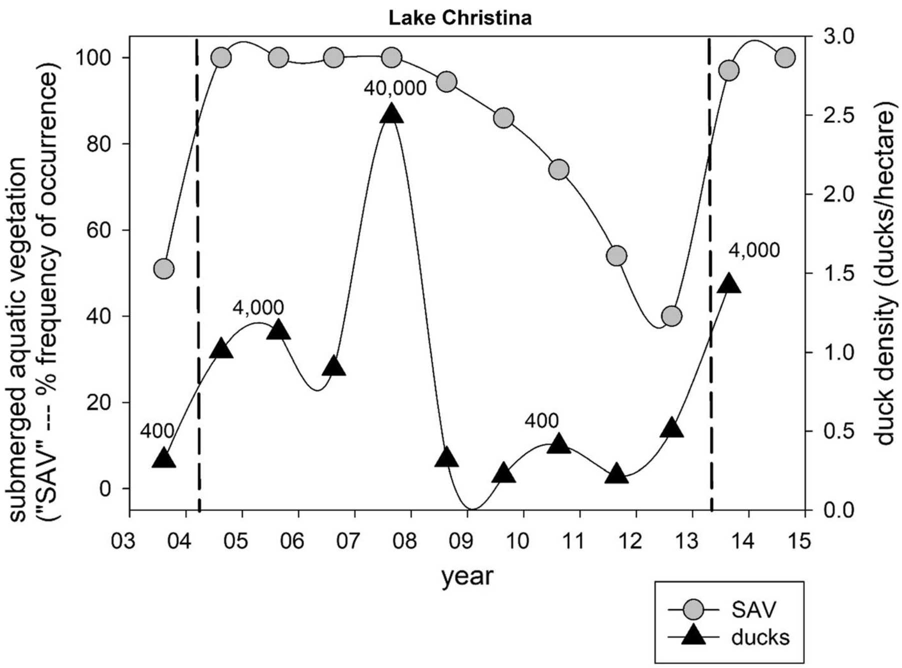

Fig. 5 Lake Christina's submerged aquatic vegetation occurrence and duck density had increased following management activities in 2004 and 2013. The dashed lines indicate the lowest water levels following drawdowns that occured in the fall 2003 and fall 2012. When submerged aquatic vegetation was ~ 50% and duck counts were ~ 400 birds, management action was triggered. After treatment in 2004, the duck density increased by one to two orders of magnitude (or, ~ 4000–40,000 birds). The influence of management on aquatic plants and waterbirds were sustained for a few years before returning to the turbid state

ecosystem services, such as improved water quality, an abundance of wild rice, and increased waterbirds for harvest and bird watching. Our results underscored how active management of lakes that are often situated within landscapes with altered hydrology and often intensive land use may be helpful in enhancing habitat and attracting waterbirds during fall migration. Monitoring and dissemination of management results is an important component of any management program to employ adaptive management strategies so that resource agencies can demonstrate the results of management investments and learn by doing.

Managed lakes typically had quality habitat and attracted ducks

Submerged aquatic vegetation structures shallow lake ecosystems because SAV responds to and integrates water chemistry and water depth (Beklioglu et al., 2006; Van Geest et al., 2007; Phillips et al., 2016). However, the literature is sparse regarding association of SAV presence or abundance with waterbird use, except for Hanson & Butler (1994b), Mitchell & Perrow (1998), Stafford et al. (2010), and Fox et al. (2018). Although waterbirds can uproot macrophytes, they are unlikely to cause a macrophyte-dominated lake to shift towards a turbid lake because removal of total plant biomass is low each season and the grazed plants are resilient (Hansel-Welch et al., 2003; Beklioglu et al., 2006; Chaichana et al., 2011). We found several waterbirds, including Coot, Ring-necked Duck, and all ducks (18 species in total) were responding strongly to high SAV coverage (Figs. 2, 3), both on managed and unmanaged lakes. This aligns with the notion that waterbirds prefer shallow lakes in clear-water states (Hanson & Butler, 1994b; Scheffer, 2004).

Although the average condition of the managed lakes resembled a turbid state (Supplementary Materials F2) and hence triggered management, the annual maximum conditions resembled a clear-water state (Scheffer, 2004). This contradiction can be explained by simple statistics (a single average value vs. annual maximum values) and the high variability in the lakes across years (Table 1). By taking repeated measures annually for 10 years, we documented that management substantially reduced water depths by an average of 150 cm, improved water quality, promoted abundant SAV and rice, and attracted waterbird use. Other studies have noted shallow water depth following experimental drawdowns as a driver in bird diversity and abundance (Colwell & Taft, 2000; Holm & Clausen, 2006). However, water depth alone did not correlate with species richness or species-specific abundances, but rather most species were responding principally to abundant SAV regardless of water depth or management. Therefore, benefits could be achieved by protecting or mimicking ecosystem processes to promote SAV, such as natural drawdown cycles and nutrient uptake, instead of simply setting pool depths for targeted species (Euliss et al., 2008). Shallow lakes in the clear-water state would benefit from protection of existing water clarity and high SAV, whereas degraded turbid-state lakes may require water depth manipulations in order to improve water clarity and SAV that predicts waterbird use. Water depth management was the tool most frequently used for improving lake condition while SAV presence was ultimately attracting large waterbird communities (Hanson & Butler, 1994b; Hargeby et al., 1994; Hansson et al., 2010).

Minnesota is a major migration corridor and harvest area for Ring-necked Ducks during fall migrations and important habitat for this species includes water depths < 150 cm, lush wild rice and SAV (Cottam, 1939; Hohman, 1985; Stathis et al., 1994). Thus, our major findings are consistent with the previous literature, and this long-term dataset was able to link active habitat management (i.e., water depth reductions to increased SAV and wild rice) and Ring-necked Duck use of managed lakes during fall migration.

Our results indicate that managing lakes for quality waterbird habitat and duck abundance might benefit waterfowl hunting. Duck abundance is correlated with hunter success and leads to greater hunter satisfaction (Schroeder et al., 2017). Mallards are the most harvested duck species within North America and Minnesota, but Mallards were not clearly responding to management or SAV. We suspect that Mallards were often feeding on nearby corn fields and not on the lakes during our aerial surveys (Sugden & Driver, 1980), but were still available for harvest. Mallards were likely underrepresented in our lakes surveys and may not be responding as strongly as some SAV-dependent bird species like Ring-necked Ducks.

Management substantially increased wild rice

Wild rice beds are declining across its historical range for a variety of reasons (Pillsbury & McGuire, 2009), and an increase in wild rice is a key management goal in Minnesota (MNDNR, 2010). At our study lakes, "management" of rice simply entailed beaver dam removal and beaver trapping in order to create ideal water levels for rice production (no water control structures were used at these lakes). High water levels or rapid water level fluctuations induced by beaver can drastically reduce rice beds (Archibold & Sutherland, 1989). Wild rice abundance was substantially greater in the study lakes that had experienced water level stability as a result of beaver and dam removal.

Interestingly, we did not detect a strong correlation with wild rice frequency of occurrence and waterbird use during the daytime. This is at odds with the expectation that wild rice is important for several species of waterbirds during fall migration (Cottam, 1939; Moyle, 1944; Hohman, 1985); for example, Minnesota's wild rice can comprise >50% of forage for some species in fall (Morse, 1941; Hohman, 1985). It is unclear whether the lack of association is due to human harvest, bird use of other food resources like corn, or detection problems during the bird surveys. Wild rice is an important grain harvested by Minnesotans (MNDNR, 2010), but the fall harvest season (August–September) does not coincide with the principal fall migration period and waterbird surveys during this study (October–November). It is not clear whether human harvest could affect duck use of these lakes later in the season. Alternatively, waterbirds may use the rice beds principally at night time when we did not survey. Our experience leads us to suggest that high density of wild rice can obscure the detection and the accuracy of the bird counts. Future bird surveys in wild rice beds could use thermal imaging at night time to reduce the detection concerns. Other studies were also unable to disentangle the effects of wild rice abundance and waterbirds (Aagaard et al., 2015, 2018). Thus, wild rice may not be a principal driver of fall waterbird use and/or bird detection issues abound.

Notes on the case studies

Lake Maria waterbird density increased significantly for 1 year following management (Fig. 4), yet Lake

Christina had high duck use sustained for many years after management (Fig. 5). We speculate that following drawdown in 2006, Lake Maria had enough water for ducks, but little water (< 1 ft) for hunter access by boat. However, by fall 2007, water levels rose and emergent vegetation was high, which allowed for high hunting pressure at this popular hunting lake. Lake Christina had lower hunting pressure than Lake Maria because Christina is five times larger, had a designated MWFRA restricted for hunting, and had scant emergent vegetation to obscure hunters. Minnesota law required hunting boats to be hidden in emergent vegetation, so lack of dense emergent beds would preclude open-water hunting. Although Lake Maria's habitat remained good for at least 8 years following management, duck density may have been high only when the lake was inaccessible to hunting. Lake Maria was a popular hunting lake and contained dense emergent vegetation that concealed hunting boats for years after management.

High duck density in 2006 at Lake Maria may not be only influenced by management, but also by weather patterns. Lake freeze-up in northern Minnesota can force birds to southern lakes that remain open. Several unmanaged lakes nearby Lake Maria also experienced an increase in waterbird use in fall 2006, likely due to ice-up conditions in the north.

Management implications

Preservation and maintenance of shallow lakes in a clear-water state is optimal, but management for wildlife habitat enhancement is needed for lakes currently in the turbid-water state. The restoration and enhancement of shallow lakes is rich in theory, but complex to thoroughly understand, monitor, implement, and repeat (in sensu Moss et al. 1996; Scheffer 2004; MNDNR 2010). The personnel (e.g., time and expertise) and infrastructure (e.g., water control structures) required to manage wildlife lakes are significant. As example, beaver and dam removal is frequently required, yet it is becoming increasingly difficult to recruit contract trappers for removal efforts. Further, many managed lakes have fish barriers and/or water control structures that require frequent monitoring and maintenance. These actions require dedicated resources to properly implement and focus on lake management. Given the resources put into managing these lakes, quality management records will help us further parse out the effects of various techniques (e.g., the differences in timing and duration of drawdowns on habitat and birds).

Trade-offs exist when using drawdown as a wildlife habitat management tool (Mitsch & Gosselink, 2015). Wildlife managers face pressures to manage shallow lakes for ecological functions, wildlife populations, and human recreation. The drawdown has benefits of recycling nutrients from undecomposed organic matter, increasing macroinvertebrates as waterbird forage, regenerating wetland seed banks, and consolidating nutrients into the sediments. However, partial and complete drawdowns have the potential to allow for invasion of undesirable plants (e.g., *Typha x glauca*), reduce piscivores that may provide top-down control of undesirable fishes, and reduce invertebrates like amphipods that are important food for migrating waterbirds (Anteau & Afton, 2008); drawdowns make lakes inaccessible for recreation, which can create public opposition. However, inaccessibility during the hunting season may allow for migratory bird resting areas during migration (see Lake Maria's results as an example).

Various waterbird species have specific requirements and preferences for water depths and in-lake habitat conditions (Baldassarre, 2014), and therefore, management will require trade-offs at the species level. Management that extends to landscapes and considers the context of the lake within a larger wetland complex could be beneficial for maximizing waterbird richness and abundance. For example, management that uses combinations of high water, partial drawdown, and complete drawdown in wetland complexes can provide habitat for a suite of species simultaneously (Colwell & Taft, 2000; Baschuk et al., 2012). We found SAV as the strongest driver of waterbird abundances, so promoting habitat conditions with high SAV can increase waterbird abundance. We found SAV can be abundant in unmanaged shallow lakes with clear and relatively deep waters (> 280 cm) or through managing lakes with drawdown and shallow waters (< 140 cm).

Before installing or removing existing water control structures, it is important to consider whether the lake can undergo wet-dry cycles with hydrologic restoration instead of ongoing management by water control structures. In this study, the lakes required structures to manage water levels because landscape-scale alterations, like consolidation drainage, made hydrologic restoration impossible. Euliss et al. (2008) warns of using structures simply to alter the water depth in order to meet short-term management goals because these actions could reduce wetland diversity and productivity over the long term. Installation of water control structures only where required and having an objective-based management plan for their use could be beneficial.

Our study found biologically significant relations between lake habitat and waterbird use in fall, both in managed and unmanaged lakes. Achieving management objectives will require an understanding of the lake's history and current conditions, as well as evaluating management actions that can create desired outcomes (Bishop et al., 1979; Euliss et al., 2008). Integrated monitoring and management programs, such as that modeled by the MNDNR Shallow Lakes Program (MNNDR, 2010), represent opportunities to effectively achieve management goals, such as waterbird habitat and abundances.

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Data availability The datasets are available through the U.S. Geological Survey's research repository (https://doi.org/10.5066/P9QJ1CBR). Please cite the data as follows: Larson, Danelle M. and Minnesota Department of Natural Resources, 2020, Shallow lake management enhanced habitat and attracted water birds during fall migration data, U.S. Geological Survey data release, https://doi.org/10.5066/P9QJ1CBR.

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