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Implications of condition shifts on shallow lakes

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Chapter 1: Review of management-related condition shifts in shallow lakes: causes, case studies, cost, and climate change.

Abstract.- Shallow lakes have undergone condition shifts throughout time by natural causes, management actions, or a combination of the two. Because shallow lakes are especially vulnerable to shifts towards turbid conditions, management actions on shallow lakes have focused on water level/retainment, biomanipulations, the management/removal of non-native species, and land-use changes. This review compiles a summary on ecosystem shifts including a discussion on the frequency of shifts historically and the importance and causes of those shifts, trophic cascades, and the influence of introduced species in shallow lakes. This review will then examine case-studies of management-linked shifts and explain current shift theory. Next, it will review cost analyses of maintaining a stable condition considering both anthropogenic decision factors and the effects of shifts on ecosystem health and services. Finally, it will discuss expected effects of climate change on shallow lakes.

Frequency and stability of shifts before industrialization compared to today

The actions of civilization have caused great change to the environment and increased the influence humans have on world systems, potentially affecting the frequency of shifts in ecosystem condition. Since the industrialization era, humans have been able to travel farther and in greater frequency. Coinciding with our attitude towards consumerism, pollution, waste, and deforestation have increased dramatically. Urbanization has also decreased the percentage of pervious surfaces, which encourage runoff events that will exacerbate future weather-related pollution and disaster events. Greenhouse gas emissions also are cause for concern. The United States Midwest, specifically, have per capita emissions of greenhouse gases more than 20% higher than the national average and an energy-intensive economy (Pryor et al. 2014). With water-intensive crops (e.g., corn) and a temperate climate, climate change will have a large effect on the sprawling fields and streams/lakes that reside there. Examples of these ecosystem influences can be found around the world. But how does the frequency of shifts today compare to pre-industrialization?

Frequency of condition shifts prior to industrialization can be determined through sediment core analyses by showing changes in zooplankton community composition. Lake Christina, a shallow lake located in western Minnesota, had a relatively stable community from 1800-1950 (Hobbs et al. 2012). A single shift in ecology was noted in 1950 ($\pm$4 years) as the sub-fossil *Bosmina* spp. densities increased. Hobbs et al. (2012) suggested this indicated anthropogenic drivers would dominate how the lake ecosystem would function from then on. Post-1950, sediment core *Bosmina* spp. densities decreased to near historic levels only during clear, macrophyte-dominated conditions, suggesting that the pre-1950 condition of Lake Christina was clear (Hobbs et al. 2012).

The history of shallow lakes management is built by individual case studies and documentation of shifts like that of Lake Christina. When viewed in combination, the summary of these case studies revealed a comprehensive trend that many shallow lakes were in a stable clear condition prior to the industrialization era (Figure 1.1). Urbanization and pollution increased, inducing a shift towards more stable turbid conditions. In response to the effects of pollution, the Clean Water Act enacted in 1977 along with conscious efforts to improve water quality conditions reduced excess nutrients and allowed some shallow lakes to transition towards a clear condition. However, once a condition is turbid due to excess nutrients, it takes extreme effort and time to shift back and, if accomplished, the condition is generally less stable. Many management actions have tried to revert changes inadvertently caused in lake condition, and the stability of the condition thereafter is often diminished. Based on climate model studies, a turbid condition in some shallow lakes may stabilize despite our best prevention efforts (Mooji et al. 2007).

Shallow lakes, ecosystem condition shifts, and the event of trophic cascades

Aquatic ecosystems exist within a gradient between clear and turbid conditions and a shift towards one end of the spectrum occurs through trophic cascades (i.e., top-down or bottom-up controls). Shifts often occur due to a disturbance or change in nutrient availability whether natural or human-related (Scheffer et al. 2001), which affect organisms living in or using that water body. Shallow lakes are vulnerable to cultural eutrophication due to their size (Cael et al. 2016). Therefore, the ecosystems of individual shallow lakes may vastly differ due to geographic location, physical, chemical, and biological properties, and their proximity to disturbed habitat. The study of condition shifts has increased within the last two decades (Figure 1.2). Within these studies, shallow lake study sites are not as common compared to deep lakes and rivers. This notion was also supported by a Google Scholar search of “ecosystem state shifts shallow “state shifts”” resulting in 108 unfiltered results compared to “ecosystem state shifts “state shifts” -shallow”, which resulted in 270 unfiltered search results. For a reference aid, Table 1.1 was compiled of shallow lakes that have had documented shifts and will be used throughout this review.

Shallow lakes are the most abundant lake type within the globe and are unique in size and characteristics (Cael et al. 2016). Published articles involving shallow lake ecosystem shifts do not state the requirements to be considered a ‘shallow’ lake other than light reaching the bottom. For consistency in this review, shallow lakes are classified as bodies of water usually 15 feet (5 meters) or less in depth and 50 acres (~20 hectares) or greater in size (MN DNR 2019). A shallow water column allows a proportionally large photic zone and littoral zone, encouraging vegetation to grow throughout the entire lake (Scheffer et al. 2001). Therefore, shallow lakes have greater productivity and act as important waterfowl habitat (Epners et al. 2010). The short water column makes shallow lakes vulnerable to sediment resuspension and increased aeration as wind easily circulates the water column, which affects the lake’s condition and its trophic levels (Havens et al. 2012, Scheffer 1998). Furthermore, frequent mixing can result in homogenous communities of smaller organisms such as zooplankton (Livings et al. 2010).

Lakes currently in a clear, macrophyte-dominated condition have lower nutrient levels and will display different characteristics than those of a turbid, algal-dominated condition with higher nutrient levels. A clear, macrophyte-dominated lake will have a high abundance of plants and lower abundance of phytoplankton because plants can use nutrients from sediments (Meerhoff and Jeppesen 2009). This will lead to a higher abundance of large zooplankton that ingest a broader range of algae and more piscivorous fish that prey on these zooplankton (Bronmark and Hansson 2005). A turbid, algal-dominated condition will tend to have turbid or cloudy, sediment-filled water and be characterized by lower plant occurrence and a higher phytoplankton abundance. The rest of the trophic levels then follow the opposite pattern of a clear condition.

A change in condition will affect all trophic levels in a trophic cascade as a positive feedback loop. As an example, once a historically clear, macrophyte-dominated lake receives excess nutrients or increased turbulence, phytoplankton will use those nutrients to increase growth. This growth of floating plant-like organisms then blocks the sunlight from reaching the lakebed, leading to decreased plant abundance (Schallenberg and Sorrell 2009; Hobbs et al. 2012). An increase in phytoplankton abundance (especially cyanobacteria and flagellates) will lead to a decreased abundance of large zooplankton (i.e., *Daphnia* spp.) due to competition with smaller zooplankton such as *Bosmina* spp. that have increased reproductive rates and a specialized foraging mode (DeMott and Kerfoot 1982). This will lead to an increase in non-piscivorous fish as they have a greater prey source, causing a decrease in piscivores due to limited resources (i.e., habitat). A dramatic decrease in nutrient availability at the initial trophic level or a decrease in non-piscivorous fish can allow the system to shift back again.

Causes of condition shifts within shallow lakes

One of the most common reasons a lake shifts condition is due to excessive phosphorous (Correll 1998). Growth within a lake is dependent on the availability of the limiting nutrient. For plant and phytoplankton growth, that limiting nutrient is often phosphorous (Kalff 2002; Miller and Spoolman 2012). If a large amount is released into a water body that cannot filter or dilute the phosphorous efficiently, an algal bloom will likely occur. This release of phosphorous may be of a natural cause through phosphorous cycles and sedimentation, internal loading conditions, fish kills, or natural physical phenomenon (Schoenebeck et al. 2012). Another possibility is the phosphorous is a direct result of anthropogenic activities including but not limited to agricultural runoff, sewage overflow, and direct dumping.

Natural causes

Phosphorous is a natural particle that is cycled into different forms and undergoes the process of sedimentation within shallow lakes (Kalff 2002; Miller and Spoolman 2012). Phosphorous is contained within organic matter and stored in rocks. Organic matter is broken down and rocks will weather over time, leading to the release of phosphorous and other elements or compounds. Runoff phosphate salts are the common form of phosphorous, which is partially soluble in a water body as an ion (Miller and Spoolman 2012). This phosphorous will then undergo sedimentation in which it attaches to soil particles floating in the water column and settles on the lakebed; a rapid process in shallow lakes (Kalff 2002). These sedimented phosphorous particles will remain at the bottom of the water body unless there is an outflux of water in the system or the sediment is resuspended through turbulence.

Even if phosphorous is not added in large amounts, historic loads can magnify the effect of additional phosphorous, also known as internal loading conditions (Meerhoff and Jeppesen 2009; Kalff 2002). Historic, in this case, is a relative term that refers to phosphorous input build up over time. Although the daily influx may not be of concern, after several days with no dilution or flushing of that phosphorous out of the system, it is additive. Systems have a threshold at which phosphorous begins to influence the organisms around it (Scheffer et al. 2001; Miller and Spoolman 2012). Once past this threshold, the lake condition adjusts to that phosphorous load with increased phytoplankton biomass.

Physical phenomena such as a fire or flooding can exaggerate the amount of phosphorous reaching a shallow lake. Wildfires reduce shoreline vegetation resulting in increased runoff and erosion (Paige and Zygmunt 2013). High winds across the shallow water body increase wave energy, leading to resuspension of sediments containing phosphorous (Havens et al. 2012; Scheffer 1998). Flooding leads to an increased water influx and greater turbulence, also leading to higher resuspension. Shallow lakes are especially vulnerable to changes caused by these phenomena because the resuspended particles are released directly to the photic zone (Kalff 2002). Summer storms are the most common disturbance for shallow lakes (Padisak et al. 1999). However, natural processes leading to phosphorous fluctuations are often small and hard to control non-point sources, while increases in phosphorous due to human activities are more noticeable condition shift events.

Anthropogenic causes

A major source of phosphorous input from humans comes from agricultural sources in the form of fertilizer and manure, which was listed as the phosphorous input in each agricultural catchment issue within Table 1.1. Fertilizer applied in the spring is frequently washed away with rain and enters a nearby lake or stream. A common practice used to be stockpiling manure year-round for later use, which exposed it to rain and melting snow (Hobbs et al. 2012). Insecticides, fungicides, herbicides, etc. containing phosphorous are widely used in agricultural practices and can adversely affect aquatic diversity, community structures, and human health (Kalff 2012). This input of phosphorous to a water body stimulates the growth of producers (Miller and Spoolman 2012) such as phytoplankton, which then encourages eutrophication by blocking sunlight from aquatic macrophytes (Schallenberg and Sorrell 2009; Hobbs et al. 2012).

Sewage system overflows are another potential source of excess phosphorous in the system as they are underbuilt for current climate conditions or have degraded over time. A study by Beenen et al. (2011) found that separate sewer systems have annual phosphorous concentrations ranging from 0.12-0.62 mg P/L on average. This was compared to a combined sewer system having an average annual phosphorous concentration of 0.63-3.40 mg P/L. The Northern Glaciated Plains ecoregion typically has average phosphorous concentrations ranging from 0.12-0.16 mg P/L (Engel et al. 2009), therefore separate sewer systems are better but both sewer systems still present an important source of phosphorous. Sewage systems are designed to handle a certain amount of discharge involving human waste, organic litter from streets, and floodwater. Once past capacity, the overflow could potentially enter the nearby lake. As this organic matter reaches the lake and begins decomposing, it gives off large amounts of phosphorous and greenhouse gas (Miller and Spoolman 2012). Therefore, improved agricultural practices and wastewater treatment can reverse eutrophication (Kalff 2002).

Direct dumping is an illegal act decreed by the Environmental Protection Agency that used to be a common practice and may still occur sparingly (Clean Water Act in 1977 published by Hall Jr. in 1978). Direct dumping is the term for organic waste poured into water bodies in hopes of diluting the pollutants. Specifically, dumping of industrial waste into the nearest water bodies was considered proper disposal. Hypoxia and algal blooms were common in lakes and rivers receiving factory effluent (Smol 2019; Kalff 2002). Although there were no instances of direct dumping found in this compilation of shallow lakes studies (Table 1.1), it is still mentioned as a potential influencer of lake condition and have previously resulted in nuisance algal blooms in other water bodies.

The reason for a condition shift in a shallow lake may be natural, human-related, or a combination of the two. Natural phosphorous influx, although important, is not easy to quantify or prevent. Therefore, management agencies have generally focused on water level and retainment for limiting eutrophication. They have also implemented land-use change and improving remaining agricultural and waste practices. Whether the cause for a shift is droughts, storms, sewage system overflows, agricultural runoff, or a combination along with others, many of these factors will increase in frequency and severity with climate change.

Species introduction

Introduced species may change an aquatic system for a variety of reasons. An introduced species is a threat to native species when they take over the same niche and don't have natural predators, competitors, parasites, or pathogens to control their population (Miller and Spoolman 2012). With less suitable habitat and prey resources, native species may be extirpated and community structure changed. Introduced species may also influence lake conditions due to behavioral traits such as bottom-feeding leading to bioturbation. Although invasive species may be introduced intentionally for a specific use (i.e., game fish, vegetation control), they may also be unintentionally spread (i.e., ship ballast waters, boat drains and sides/trailers). Hereafter details the prevalence, effects on biota and shallow lake condition, and past and present management for a few invasive species. Although prevalence is not documented for shallow lakes, this section will describe potential effects of select invasive species on lake conditions.

Invasive species that have been known to cause a shift towards turbid conditions include Common Carp *Cyprinus carpio,* and Rusty Crayfish *Faxonius rusticus* (formerly *Orconectes rusticus*). Common Carp have expanded into every state in the US except Alaska (Nico et al. 2020), whereas Rusty Crayfish's dominance is not nearly as drastic (Donahou et al. 2020). Common Carp introduce bioturbation (Garcia-Berthou 2001) and affect phytoplankton abundance and diversity through benthic foraging (Weber and Brown 2009). Resulting winter kill events also contribute large quantities of nutrients from decomposing carcasses (Schoenebeck et al. 2012). Zooplankton and benthic invertebrates are affected through predation and reduced foraging efficiency (Weber and Brown 2009). Adult carp move into shallow lakes to spawn in the spring, especially following severe winter hypoxia, to exploit nursery habitat that is relatively free of predators (Bajer and Sorensen 2010). These shallow lakes may also be turbid due to Rusty Crayfish. Wilson et al. (2004) found submerged macrophyte species richness declined as much as 80% from the crayfish grazing on periphyton or uprooting seedlings and established plants. Their presence also causes a decline in non-piscivorous fish and snails that share their prey preferences (Wilson et al. 2004).

According to a study by Bajer et al. (2009) a one-year increase from ~30kg/ha to ~100kg/ha of Common Carp decreased vegetation and waterfowl use by 50% and the next year's increase to 250 kg/ha decreased the vegetative cover to 17% of lake surface area and waterfowl use to ~10% of original value. This does not bode well for Midwest shallow lakes as Common Carp biomass is typically 300-400 kg/ha (Bajer et al. 2009; Koupal et al. 2013) and Common Carp can represent a large proportion of the total fish biomass (e.g., >90%, Schoenebeck et al. 2012). Common Carp management methods have included separation cages, pheromone-lure traps, commercial harvest, water-level manipulation, cyprinid herpesvirus-3, and sex ratio manipulation, but successful removal of Common Carp has required repeated and intensive interventions (Pearson et al. 2019). Pearson and colleagues (2019) modeled embryo electroshocking, juvenile trapping, and increasing avian predation individually and combined with commercial harvest efforts and concluded these methods also needed a substantial input of effort. Common Carp could be removed through biomanipulations like those in Table 1.1 for Bream and Roach, but clear conditions from biomanipulations have not been recorded to last more than a couple years (Hobbs et al. 2012). Rusty Crayfish have been easier to remove as a study by Hansen et al. (2013) observed Rusty Crayfish abundance declined by 99% in eight years with no compensating recruitment observed or significant increase in abundance four years later. Native sunfish *Lepomis* spp. and crayfish *Orconectes virilis* increased by 100% and in 2-4 meters of water, macrophytes increased significantly (Hansen et al. 2013). Encouraging natural predation on small crayfish through angling restrictions has been documented to cause large declines in Rusty Crayfish populations, but trapping and manual removal have been the most efficient method of control (Hein et al. 2006).

Invasive species that encourage clear condition include Zebra Mussels *Dreissena polymorpha* and Eurasian watermilfoil *Myriophyllum spicatum*. Zebra Mussels have dominated the Great Lakes (Benson et al. 2020) since first being documented in 1988, causing competition for native mussels and impairing water delivery for municipal, hydroelectric, and industrial pipe users (MacIsaac 1996). Due to their sessile nature, Zebra Mussels filter large amounts of plankton and detritus from the water column (Bruner et al. 1994; Fahnenstiel et al. 1995), thus decreasing chlorophyll concentrations and phytoplankton productivity. Following Zebra Mussel introductions in Oneida Lake, New York, average depth receiving 1% surface light expanded in area by 23%, max macrophyte depth increased by 2.1 meters, and the macrophyte community species richness increased and changed from low-light tolerant species to those with a wider range (Zhu et al. 2006). However, waterfowl using those shallow lakes showed elevated concentrations of organic pesticides and polychlorinated biphenyl compounds after eating contaminated Zebra Mussels (MacIsaac 1996). There are few examples where Zebra Mussels were managed or removed without ecological destruction and have so far been managed by scuba diving (Wimbush et al. 2009) and through scrubbing and quarantine of unionids infested by Zebra Mussels (Patterson et al. 1997).

Eurasian watermilfoil was introduced in the US in the early 1900s spreading to 47 states by 2020 (Pfingsten et al. 2020). Eurasian watermilfoil is very efficient at up-taking phosphorous, limiting algal growth and improving water clarity while decreasing the species richness of other plants. Rapid dominance of Eurasian watermilfoil in eutrophic systems often occurs after disturbances, such as water level changes or macrophyte composition shifts (Smith and Barko 1990). Smith and Barko (1990) found that moderately turbid shallow lakes therefore experience the most milfoil growth and encourage canopy formation through nutrient-rich sediments. Abundant growth of this and other submersed plants may interfere with swimming and boating, reduce aesthetic appeal of water bodies and quality of sport fisheries, lower dissolved oxygen, and increase mosquito abundance (Smith and Barko 1990). Current control techniques (such as systemic herbicides, diver dredging, bottom barrier replacement, and derooting) are short-lived and expensive, while other control measures such as derooting, shallow dredging and drawdown may instead encourage propagation (Smith and Barko 1990).

Curly-leaf pondweed *Potamogeton crispus* behaves as a winter annual in northern lakes and plants rapidly senesce and decay in midsummer, contributing to nutrient recycling and algal blooms (Johnson et al. 2012). Curly-leaf pondweed is highly spread throughout the contiguous US, especially surrounding the Great Lakes and along the Western coast (Thayer et al. 2020). Specifically, it was noted in over 730 Minnesota lakes in 2011, mostly avoiding the northern region of the state (Heiskary and Valley 2012). Heiskary and Valley (2012) found shallow lakes with minimal native vegetation typically have algal blooms following curly-leaf pondweed decay, whereas abundant native vegetation dampens this effect. Heiskary and Valley (2012) suggest a lack of plants in the water column allowed increased wind-related mixing or bioturbation (Weber and Brown 2009) or that zooplankton lost their refuge and were more susceptible to fish predation, rather than curly-leaf pondweed being the direct culprit to increased turbidity (Schriver et al. 1995). Experimental whole-lake treatments of curly-leaf pondweed showed little evidence of improving water quality (Welling 2010) and Heiskary and Valley (2012) stated removing large areas without replacement of other vegetation could degrade water quality and fish habitat greater than no management (Valley et al. 2004; Kovalenko et al. 2010). Curly-leaf pondweed provides habitat for native piscivorous fish in lakes that, due to their phosphorous loading, would otherwise have no vegetation (Heiskary and Valley 2012). A Sentinel Lakes study concluded there was little evidence supporting curly-leaf pondweed as a driver of water quality and managers should not expect water quality improvement without long-term reductions in internal and external phosphorous loads (Heiskary and Valley 2012). Management of curly-leaf pondweed includes low-dose herbicide treatments (i.e., fluridone, endothall) in early spring to control its early season growth (Johnson et al. 2012), which has successfully decreased sprouting after multiple years of treatment and extensively reduced biomass within each year of treatment (Skogerboe et al. 2008). Early season, low dose treatments can control curly-leaf pondweed biomass and reduce abundance of turions (like seeds) in lake sediments more effectively than later, more concentrated treatments (Johnson et al. 2012). Critical number of treatment years to achieve long-term control is unknown.

Invasive species like the Common Carp, Rusty Crayfish, Zebra Mussel, Eurasian watermilfoil, and curly-leaf pondweed can affect the condition and condition stability of a shallow lake. Common Carp and Rusty Crayfish encourage a lake to shift towards a turbid condition, while Zebra Mussels and Eurasian watermilfoil encourage a clear condition.

Whether curly-leaf pondweed should be placed with those that shift a lake towards turbidity is debatable. Each invasive species has direct and indirect influences on ecosystems that continue to be discovered and explored. These species may have been dispersed naturally, by humans, or a combination of the two and have enhanced effects on a shallow lake ecosystem. Efficient management of these invasive species is still being explored and will be increasingly important as their prevalence increases in shallow lakes.

Management actions

Within the lakes listed in Table 1.1, there were 25 management-related shifts documented. Of those lakes listed, 90% were considered important waterfowl habitat and 50% were used as a fishery. Seventy-two percent of management actions shifted the lake towards clear conditions. The number of actions causing turbid conditions before 1970 was equal to the number of actions causing a turbid condition 1970 and later. The two most popular management action categories were water level or retainment methods and biomanipulation actions at 36% (Figure 1.3). Land-use related actions were the next most common (20%), trailing by four events, which mainly involved rehabilitation and reduction of agricultural nutrients, and fixing wastewater and sewer system effluence to control phosphorous input. Finally, two cases were an invasive species establishment (8%).

The water level or water retainment related management actions included dam construction, water level drawdowns, flushing, and dredging. Dam construction commonly occurred during the industrialization period for power and to conserve water during droughts, like on Lake Christina, which altered hydrology and led to a turbid condition (Hobbs et al. 2012). On the upstream portion of a dam, water and sediment flows at a slower rate and pools above the typical flood banks into the floodplain (Grant et al. 2003). The floodplain vegetation gradually dies out from the submersion in water paired with lowered carbon dioxide and sunlight. The dam’s downstream water volume decreases and causes the banks to narrow, exposing land to dry and eventually develop riparian vegetation. The increased residence time for water leads to warmer water temperature and less variation in flood events, which creates an enhanced breeding ground for invasive species compared to the native biota who may have a lower tolerance (Kedra and Wiejaczka 2018). This artificial water level stabilization also encourages the shallow lakes in agricultural areas to shift into a permanently turbid condition (Scheffer and Jeppesen

2007). However, dams have potential to weaken water temperature warming trends related to climate change and, if appropriately managed, have the potential to release colder water for maintaining native aquatic organism presence (Kedra and Wiejaczka 2018).

Water level drawdowns, system flushing, and dredging are three other actions that have been known to shift a shallow lake towards a clear condition (Table 1.1). A meta-analysis of 70 lakes found water level drawdowns in dry summers was the main trigger for a shift towards a clear condition that would have otherwise been in a stable turbid condition (Scheffer and Jeppesen 2007). Lower water levels allow deeper sunlight penetration and increased aquatic plant growth, encouraging a shift towards a clear condition (McGowan et al. 2005). Excessive nutrients and internal loading can also be combatted in shallow lakes by flushing the system, acting as a reset button on the eutrophication process. Furthermore, flushing a shallow lake can prevent toxic Cyanophyta (blue-green algae) from establishing as they are intolerant to sudden environmental changes (Padisak et al. 1999). Finally, dredging is a process to clear out the lakebed by removing sediment containing nutrients and decaying matter. Therefore, it effectively lowers turbidity by reducing nutrient recycling and sediment resuspension (Hanson and Stefan 1985).

Biomanipulation is the other most common management action performed to induce a shift (Table 1.1). Biomanipulation is also the most common action that has occurred within the last few decades and seems to be the preferred present-day method of inducing a shift towards a clear condition because it is the most cost-effective and successful. This action usually involves a manipulated reduction in planktivorous and benthivorous fish, which has been known to lead to reduced plankton biomass through *Daphnia* spp. grazing and a decrease in macrophyte uprooting and sediment resuspension, respectively (Bronmark and Hansson 2005). Specific examples noted were reduced Bream *Abramis brama* stock in Lake Veluwe (Ibelings et al. 2007) and Bream and Roach *Rutilus rutilus* in Lake Wolderwijd (Meijer and Hosper 1997). Lake Christina underwent multiple chemical biomanipulations, which was especially detrimental to the planktivorous fish populations (Table 1.1). An action that is less common, due to the intense physical demand, was documented in Cockshoot Broad located in Norfolk, United Kingdom, in which management agencies manually removed the fish community (Moss et al. 1996). Although biomanipulation in the fish community is common, the stability of the resulting clear condition is variable. It is also noted that if *Daphnia* spp. are limited by the salinity levels of the lake, a fish biomanipulation meant to induce a cascade may be unsuccessful (Scheffer and Jeppesen 2007).

Case studies of documented shifts in shallow lakes

Although long-term documentations of these shifts are rare, there have been a few case studies in which the condition of a shallow lake was studied in perspective of a shift. Many reasons exist as to why these studies are so few including a lack of funding, coordination, and the complexity of shifts. Shallow lakes are often overlooked by researchers to focus on larger bodies of water where an ecosystem condition is more stable. However, studies have been conducted on Lake Shaokatan, Lake Christina, and Lake Veluwe and will be summarized hereafter.

Lake Shaokatan

Lake Shaokatan, located in Southwestern Minnesota, is a shallow lake that underwent a steady shift towards a clear condition from management action in the early 21st century. A sediment core analysis showed the pre-settlement diatom assemblages are quite different than modern assemblages in Lake Shaokatan (Edlund and Kingston 2004). This evidence for a shift towards a turbid condition after initial settlement is also supported by a study conducted in 2003 by Edlund and Kingston (2004), which showed Lake Shaokatan had a much lower concentration of total phosphorous before settlement (50 ppb) compared to modern concentrations (107 ppb). Management actions imposed to combat the decades of eutrophication were rehabilitating wetland areas, animal feedlots, and shoreline septic systems (MPCA 2009). These actions aimed for a shift towards a clear condition to provide better habitat for waterfowl use and the walleye fishery.

The land-use changes enforced to shift Lake Shaokatan into a clear condition occurred throughout the 1990s into the early 2000s. One of the actions was to rehabilitate three wetland areas, which was shown to mitigate greenhouse gases ($171-$222/ha value gained), retain runoff nutrients from agricultural lands ($1248/ha), and serve as waterfowl habitat ($16/ha) by a wetland restoration study (Jenkins et al. 2010). These values were monetized from environmental economics literature and ecosystem markets by Jenkins et al. (2010) who concluded restoration of wetlands, specifically, returns value within a year.

Four feedlots were then rehabilitated, which could reduce phosphorous runoff by 29.9% and ammonium nitrogen by 31.8% if bordered by vegetative filter strips (Rahman 2012). Finally, degrading shoreline septic systems are often associated with filamentous green algae rather than diatoms and greater detritivore abundance (Rosenberger et al. 2008). These combined actions successfully decreased phosphorous loads near the ecoregion-based standard of 90 µg/L in 1994 compared to previous years having 200-350 µg/L (MPCA 2009), which cleared up nuisance algal blooms. However, an abandoned feedlot continued to delay plants from rooting and increased phosphorous and chlorophyll-a concentrations in 1999 until it was improved in 2001. Lake Shaokatan was listed as impaired and underwent a TMDL study to find a nutrient goal for a clear condition. Water quality standards were met in 2014-2015 and current data continues to suggest these management actions allowed a clear condition to exist.

In a report by Heiskary et al. (2016) blue-green algae dominated the 2013-2014 June-September phytoplankton communities, however, there were no nuisance blooms. Algal biomass was also lower in 2014 and contained prominent cryptophytes and diatoms. Zooplankton biomass also dropped from >3000 µg/L to a max of 500 µg/L in 2014. Heiskary et al. (2016) explained the lower biomass and lack of large daphnids were most likely due to the low algal biomass and lack of previously dominant blue-green algae *Aphanizomenon flos-aquae,* which accounted for over 80% of algal abundance in 2013 (July-September). It was hypothesized that there was insufficient food or inadequate refugia from the present rooted plants to support *Daphnia* spp. Total phosphorous also decreased from >75 µg/L in 2013 to 33 µg/L in 2014 aiding the lack of blue-green nuisance blooms, attributed to changes in nutrient loading and subsequent expansion of macrophytes. It should be noted that in the summer of 2019, 15% of the lake surface area was chemically treated for plant reduction and effects have not yet been noted.

Lake Christina

Lake Christina is a shallow lake also located in Western Minnesota, USA that has had over 90 years of management action-related shifts. Lake Christina is divided into two sub-basins, which reflected different responses in sediment-core analyses. The smaller and deeper Eastern sub-basin showed heavy external influence, especially from post-settlement land-use changes nearby (Theissen et al. 2012). The shallower and larger Western sub-basin, however, showed a strong response to internal processes. Theissen et al. (2012) concluded human management of the lake has diminished the importance of natural causes for shifts over time.

The first documented human-related shift on Lake Christina was noted in 1936 after a dam was constructed (Hobbs et al. 2012), and an additional dam was constructed on Pelican Lake downstream which has a large influence on Lake Christina's water level (Nicholas Brown 2 July 2021, MN DNR, personal communication). Although it was noted by Hobbs et al. (2012) that agricultural land use and increased waterfowl populations may have started the eutrophication previously, the dam construction showed a drastic effect. Along with increased regional humidity, the lake's typical depth was doubled, initiating a reduction in phytoplankton grazers due to non-piscivorous fish expansion (Hobbs et al. 2012). Land-clearing and agricultural practices further encouraged phytoplankton dominance post-1950s, exemplified by significant shifts in $\delta^{15}N$ in sediment core analyses (Theissen et al. 2012). It's initial shift towards a turbid ecosystem from fertilizer runoff was undesirable, as Lake Christina is an important feeding and staging area for waterfowl migration in the Mississippi Flyway (Hobbs et al. 2012). Since then, Lake Christina has continuously shifted between conditions with biomanipulations of fish by management agencies instigating a shift towards a clear condition.

Management periodically reduced fish biomass in Lake Christina (Nov. 1965, Oct. 1987, Oct. 2003), which represents a top-down control as fish control *Daphnia* spp.in the absence of plants and are central to maintaining a turbid state (Scheffer et al. 2001). In conjunction with a decrease in percent landcover of cultivated land in the surrounding area, Lake Christina temporarily shifted to a clear condition for 5-10 years after each reduction (Hobbs et al. 2012). Largemouth Bass *Micropterus salmoides* and Walleye *Sander vitreus* were stocked in this lake to boost the fishery and control planktivorous species a few times after 1987, although neither were very successful. A winter refuge area was aerated in 1994 to aid the piscivores' survival but was immediately discontinued. Hobbs et al. (2012) stated the lake's phytoplankton growth is limited by phosphorous and Lake Christina remains eutrophic, but clear conditions had lower concentrations of chlorophyll-a and total phosphorous while *Daphnia* spp. showed greater abundance over *Bosmina* spp.

Lake Veluwe

Lake Veluwe is a shallow lake located in the Netherlands that has experienced management-induced shifts for over 30 years. The initial human-related shift was towards a turbid condition due to nutrient loading from agricultural streams and waste-water treatment plants' effluence in the late 1960's and completed in the 1970's (Ibelings et al. 2007). A nationwide policy was implemented in 1980 to reduce nutrient loading, but the turbid condition in many of the Dutch lakes has remained stable and resistant to efforts like biomanipulation and flushing. Lake Veluwe, however, was able to achieve a clear condition in 1979 through winter flushing of lowlands and waterways and reduced agricultural catchment nutrient loading (Ibelings et al. 2007). Hosper and Meyer (1986) confirmed the phosphorous loading of the lake was reduced through these actions from approximately 3 to 1 g P/m^{2}a (grams phosphorous per square meter of surface acre).

Lake Veluwe continued to be flushed in the winter with water low in phosphorous and high in calcium to interrupt the almost constant algal bloom it had undergone. Hosper and Meyer (1986) found these measures significantly changed the lake after 1980. Summer chlorophyll-a concentrations decreased from 200-400 mg/m^3 to 50-150 mg/m^3 and total phosphorous dropped from 0.4-0.6 mg P/L to 0.1-0.2 mg P/L (Hosper and Meyer 1986). Transparency of the lake did not improve as much, increasing from 15-25 cm to 25-45 cm, but the summer of 1985 showed a dominance of green algae and diatoms for the first time in ~20 years. These results encouraged further management action for a clear condition.

Within the 1990's, Lake Veluwe underwent a series of biomanipulations thanks to its commercial fishery (Ibleings et al. 2007). A commercial fishery introduced for Bream *Abramis brama* populations accomplished a reduction of ~30 kg/ha per year from 1993-1996. Total fish biomass was reduced to 35% of its original value and allowed expansion of *Chara aspera* dominated macrophyte beds, which were limited by sediment disturbance and reduced transparency from the Bream (Lammens et al. 2004). The reduction of Bream encouraged Zebra Mussels *Dreissena polymorpha* to establish in 1996 furthering the clear condition and although large-scale dredging in 2002 caused a temporary turbid condition, Lake Veluwe remains in a clear condition today (Ibelings et al. 2007). Ibelings et al. (2007) declared unless total phosphorous is very low, only internal macrophyte coverage exceeding 30% can achieve a lake transparency greater than one meter.

Although, long-term studies on shallow lakes are rare, these case studies show that shallow lakes are commonly affected by human actions. Settlement has introduced non-point sources of phosphorous and altered the natural hydrology. However, these stories show that eutrophication reversal is possible to maintain a clear condition and encourage fisheries and waterfowl use. Therefore, researchers should continue to study shallow lakes, which provide important ecosystem services and wildlife habitat. Whether by land-use changes in Lake Shaokatan, fish biomanipulations in Lake Christina, or flushing and benthivore control in Lake Veluwe, management actions can successfully combat nuisance algal blooms.

Shift theory – resilience and switch points

Although the causes of shifts in lake conditions are previously explained, the requirements or precipice at which a shift occurs are less known. The current theory of condition or state shifts suggests that for each condition there is a switch point or precipice at which the lake will begin the cascade towards the other condition (Scheffer et al. 2001). To intentionally shift a system back to its previous condition, the circumstances must be like before the first switch point. For example, if wanting to turn the lake back into a clear, macrophyte-dominated condition, phosphorous levels would have to be well below the threshold at which the shift began. Based on evidence presented previously in this paper, engineered shifts are possible but may not always be successful. According to van Nes et al. (2007), plotting macrophyte coverage versus total phosphorous can show the approximate range for alternative stable conditions.

This theory also discusses systems having less resilience due to the influx of nutrients or invasive species (Scheffer et al. 2001). Resilience is a term used to describe how well a system will remain in the current condition. If management is attempting to shift a shallow lake back towards a clear condition but runoff nutrients are not reduced, the lake may stay in a turbid condition. However, the lake will be more willing to shift if nutrient level is reduced drastically. Invasive species such as Common Carp disturbing the sediments increase nutrients in the water column and allows a turbid condition to be more resilient to change. This increase in non-piscivorous fish will also lead to the stabilization of a turbid condition through food chain responses. Lake Veluwe’s present clear condition was determined to be dependent on the success of keystone species *Chara* (stoneworts) and Zebra Mussels (Ibelings et al. 2007). Ibelings and colleagues (2007) claimed management of these species is as important as control of excess nutrients.

Cost analysis of shallow lake management: human benefit vs. ecosystem health

Decision-makers in management positions must weigh or regard anthropogenic concerns and benefits against ecosystem function and health in accordance with each water quality condition. Management officials aim for the preservation and restoration of the environment. However, the wishes of the public sometimes conflict with what would be present in the ecosystem in the absence of humans. Most programs are funded by public funds and therefore must also keep the public content. Ideally, a compromise between human use and ecosystem health allows both to benefit. However, the term cost used here is not only in monetary value, as ecosystems provide many priceless services as well as recreational uses.

Anthropogenic decision factors

Management must weigh importance of recreational swimming and drinking-quality with wishes of anglers and boat-users. There are different standards to be met depending on the planned use of the shallow lake (MPCA 2016). A turbid condition tends to show a higher frequency in harmful algal blooms that produce cyanotoxins, which can be dangerous to consume for animals and humans. Therefore, a clear, macrophyte-dominated condition is ideal for the purposes of recreational swimming and drinking-quality. However, a surface-matted macrophyte bed may lead to conflict due to the shallow water column of the lake, as anglers and boat-users with outboard motors get tangled in the vegetation. Standards for depth include that shores for swimming should have a max depth of 1.5 m and a gradual slope, while watercraft navigation requires 0.6-1.5 m (Hanson and Stefan 1985). Angling for piscivores is more difficult in an algal-dominated condition due to the previous statement that benthivores and planktivores thrive. So, there may already be conflict between those who are using the lake directly.

Management decisions may also compare generated food and revenue from agricultural or industrial activity near the water body to the cost of maintenance for the preferred lake condition. Although agriculture and industrial activity often leads to pollution, many projects work with farmers on reducing their phosphorous contributions through buffer zones, greater efficiency in fertilizer application, riparian vegetation management, etc. (Aguiar Jr. et al. 2015). These actions lessen or slow runoff, reducing bank erosion and the introduction of fertilizer to nearby streams and other water bodies. Decreasing the percent coverage of agriculture in the surrounding watershed must balance the water body's benefits and profits of the farmers who will want compensation for converting their land. So, there are also challenges between management agencies and those not intentionally using the lake.

When management has decided to take a direct action, the monetary cost and efficiency at inducing an intended shift must be considered. For example, dredging requires a material disposal site, a dredgeable material survey to determine sediment removal volume, a post-operation depth survey and water quality monitoring thereafter (Hanson and Stefan 1985). Hanson and Stefan (1985) also explained that for large dredging projects, contracting for the work may be more expensive than buying and reselling the equipment. In contrast, although biomanipulations may need to be repeated, it is proven to show results and is relatively inexpensive (Hansson et al. 1998). Hansson et al. (1998) recommend biomanipulations should reduce planktivorous fish biomass by 75% or more within 1-3 years and efforts to reduce benthivores, young of year fish recruitment and external nutrient input (P and N) should improve establishment of submerged macrophytes. If the management decision is to control macrophyte density to mitigate boat use issues, they may choose between chemical treatment or manual removal and must decide how much of the vegetation to clear. It is better to keep parts of the lake free of aquatic plants, but still allow other parts to have dense vegetation (van Nes et al. 1999). Finally, ecosystem services are important for management decisions because demands often come from stakeholders with differing interests (Hein 2006).

Shift influence on ecosystem services and health

Ecosystem health and biodiversity are greatly affected by condition shifts as well as the specific condition the lake resides. A shift towards a turbid condition results in a loss of biodiversity, especially at higher trophic levels (Hilt et al. 2017). The clear, macrophyte-dominated state, however, is beneficial for most aquatic organisms. Primary productivity of a clear water condition was determined to be greater than a phytoplankton-dominated condition (Brothers et al. 2013). This can be explained by the increased light penetration and internal load of phosphorous available to those plants that are rooted in the soil. Due to factors that make a clear condition more enticing (i.e., aesthetics, recreational use, etc.), many management actions encourage a clear condition. However, these induced shifts, whether towards clear or turbid condition, will also have a less obvious large-scale effect.

Management-induced shifts may affect genetic diversity, adaptation to condition changes, and resistance towards invasive species. Genetic diversity of recovered dominant macrophyte species is lower in a lake that recently shifted from a turbid to a clear condition than lakes in a clear condition that have not shifted recently (Hilt et al. 2013). This follows the basic rules of succession often explained in ecology textbooks through forest succession. Genetic adaptation by phytoplankton to macrophyte allelochemicals also do not always occur after a shift (Eigemann et al. 2013). Allelochemicals are a type of inhibitory or stimulating chemical released by one plant that affects another (Hu and Hong 2008). In this case, some macrophytes give off allelochemicals that inhibit phytoplankton growth. These allelochemicals may present a solution to maintaining a clear condition and aid in resistance towards some invasive species as Vermonden et al. (2010) noted non-native macroinvertebrates thrived under phytoplankton dominance rather than macrophyte dominance.

Many areas of research on ecosystem shifts could be vastly improved upon. Effects of condition shifts on the abundance and diversity of parasites, viruses, and pathogens are not well known (Hilt et al. 2017). Therefore, the health of aquatic organisms and humans may be influenced depending on the lake condition. Information is also lacking on the ability of invasive species to establish in shallow lakes during or after shifts beyond the resilience theory presented earlier. Although many species have been shown to initiate shifts, it is unknown whether frequent shifts or a stable shift allow invasive species to establish more effectively. Specific ecosystem services are also less known and tend to be overlooked compared to shift causes.

A meta-analysis was conducted by Hilt et al. (2017) on the consequences of condition shifts for landscape carbon processing (an important ecosystem service) and results were often conflicted most likely due to the diverse assumptions and methodologies used. Hilt et al. (2017) noted that periphyton (attached algae) production was excluded or questionably presented, even though they carry out the most primary production in eutrophic lakes (Vadeboncoeur et al. 2008; Brothers et al. 2013). Condition shifts may also affect carbon burial rates (removal of organic carbon into sediments) and since primary production affects oxygen production, sediment source and oxygen exposure time are important factors for carbon burial (Sobek et al. 2009). However, a significant link was not found between carbon burial rates and primary-producer dominance (Zimmer et al. 2016). Additionally, Brothers et al. (2013) noted a significant increase in carbon burial in a turbid lake during a loss of submerged macrophytes, which contradicts the idea that sediments are held in place by macrophyte root systems and therefore allows carbon to remain buried. However, Zimmer et al. (2015) stated they found no difference in respiration, gross primary production, or net aquatic production and the two conditions showed uniform carbon fluxes despite community structure differences. If carbon processing may be affected, other processes such as greenhouse gas emissions may also be affected.

Information from this meta-analysis on the impact of condition shifts on greenhouses gases is also conflicting (Hilt et al. 2017). Emissions of carbon dioxide decrease with an increased macrophyte biomass (Kosten et al. 2010; Xing et al. 2006). However, low hypolimnetic oxygen concentrations lower benthic mineralization rates, which are responsible for lower emissions from phytoplankton-dominated lakes (Brothers et al. 2013). Increased CO_2 emissions is a consequence of the decrease in primary production when macrophyte beds have not fully recovered after a shift towards a clear lake condition (Jeppesen et al. 2016). Methane is another greenhouse gas that may be stimulated or reduced through the promotion of anoxic conditions and production of organic matter (Veraart et al. 2011). Higher and lower CH_4 emissions have been reported in areas of dense and absent macrophyte vegetation beds (Kosten et al. 2016). A major source of CH_4 is also related to ebullition (bubbles rising from the sediments to the atmosphere), but the scarcity of reliable data leaves the impact of condition shifts on emissions in question. Most studies also don’t perform a full analysis of CO_2, CH_4, or N_2O emissions (Hilt et al. 2017).

Management agencies have a lot of factors to consider when making decisions in both the cost-effectiveness and ecosystem health/service views. Depending on the intended use of the lake, standards to be met will differ and a community with differing uses may not agree on how the system should be managed. Biomanipulations seem to be the most common and effective method to induce a shallow lake into a clear condition. An induced shift, however, will have effects on the biodiversity of the ecosystem, carbon processing, and the emission of greenhouse gases by that system. These ecosystem influences will continue to be important as the effects of climate change increase in severity.

Expected outcomes of climate change on shifts

Climate change will have a great influence on shallow lakes moving forward and may cause shifts toward a turbid, algal-dominated condition to be more common. Zia et al. (2016) stated climate change will cause higher-intensity precipitation and highly variable temperature regimes. Pryor et al. (2014) agreed that over the last century, extreme rainfall events and flooding have increased and will continue to decline water quality, increase erosion, and negatively impact human health, agriculture, transportation, and infrastructure. Climate was determined to have greater influence on runoff magnitude and seasonality projections than landcover (Zia et al. 2016). These increases in rainfall and flooding events will allow a greater flux of non-point source pollutions. Previous flooding events in aquaculture has allowed invasive species to expand into new territories, bringing diseases, parasites, and pathogens with them to infect native communities (Callaway et al. 2012). The connection of normally disjunct water bodies will allow greater movement of otherwise isolated communities (i.e., carp moving over dammed areas).

Climate change also encourages warmer surface waters, longer ice-free periods, and enhanced thermal stratification. These anomalies encourage cyanobacterial blooms without the requirement of nutrient addition (Smol 2019). Temperature increases will also affect the range and distribution of specialized fish species and allow for greater establishment of invasive species (Pryor et al. 2014). Food chains, life history traits (i.e., body size), respiration and growth of organisms and ecosystem metabolism will also be affected (Jeppesen et al. 2012). These factors suggest that a shift towards turbid conditions will increase in probability in the future and maintaining a clear condition will require more from management, if it is even possible.

A review by Jeppesen et al. (2012) observed climate change effects on shallow lakes and is hereafter summarized. Sediment resuspension increases with more precipitation and changes in fish community, which exacerbates the internal loading already suffering from higher decomposition rates. Competition for light is enhanced due to increased turbidity (more runoff, changing condition, and/or change in trophic structure) and free-floating plants will be better suited. Lower submerged plant biomass is hypothesized due to higher sensitivity and turbidity or shorter winters leading to less fish kills and greater bioturbation. Phytoplankton biomass and cyanobacteria will increase and have enhanced allelopathy. Zooplankton will have a reduced biomass and grazing capacity while their plant refuge will be decreased or change in phenology. Fish will also be smaller, tend to utilize omnivory, and face greater competition due to higher metabolisms. Finally, pelagic production will dominate over benthic production. This may affect the condition stability and increase a system's sensitivity to fish kills and nutrient loading.

Climate change may be the greatest obstacle that shallow lakes have yet to face. Greater frequency and severity of storms and rain events will increase turbidity, instigating shifts towards a turbid condition. Higher temperatures and longer ice-free periods will also allow cyanobacteria to thrive, further limiting plant growth and dominance. And fish communities will change in structure and size, dealing with increased pressure for competition and less fish kills to regulate said communities. These conditions will also favor the dominance and expansion of non-native species, who disperse disease and parasites to other fish already struggling with changes in habitat, temperature, and metabolism.

Concluding thoughts

Condition shifts is a complicated topic that is gaining interest but requires further research to fill in knowledge gaps. When dealing with ecosystems in general, but especially in relation to condition shifts, the processes and factors coming into play are diverse and often uncontrollable. A lake, for example, may shift from introduced species, human-related pollution, natural physical phenomena, internal loading, etc. or a combination of these. The process of a condition shift is also not black or white but exists on a continuum. Therefore, a water body appearing in a clear condition may be reaching the threshold of the other condition. An action or event may then act as an exacerbation rather than a true causation. Although pollution was extensively mentioned, it is not always the sole reason these shifts occur. However, agencies are working to combat pollution, promote healthy ecosystems, and meet the uses of stakeholders. Furthermore, climate change will prove to be a combatting force for both aquatic organisms and humans alike.

Based on the research conducted for this review, the most common management actions are biomanipulations and water level/retainment. This suggests that land-use changes may not be as feasible, especially if agricultural practices will intensify to meet food demands in the future. Fish biomanipulations have been the most effective management action for instigating a condition shift. There have been multiple studies of success in shallow lakes and these shifts tend to be more drastic and noticeable compared to reducing nutrients. Water level management may be effective if there is a dam or some type of man-made structure to allow fluctuations and periodic outflows to release trapped sediments and nutrients. However, if the water management is attempting to flush blue-green algae blooms, it will take frequent flushes throughout the summer. Therefore, biomanipulations should be the preferred action.

Although land use change and the control of nutrients is said to be less important than climate change and equally important as keystone species management, it should not be discarded as an option. Current research into better irrigation, fertilizer application, etc. is successfully reducing loss of nutrients to surface waters. Vegetative strips should be encouraged as buffers around all water bodies to prepare for the predicted storms to come. The Midwest US has been focusing on streams near agricultural fields, but these should also be strengthened next to lakes and ponds. Research should also investigate prioritizing which water bodies will be most susceptible to climate change and focus management on those.

Invasive species will also continue to threaten the stability of condition in lakes. Based on literature describing the effectiveness of removal and influences on lake biota, Common Carp and Eurasian watermilfoil are the most concerning. Common Carp recruitment is most successful after severe hypoxia in interconnected shallow lakes and increased rain events from climate change makes disconnecting those shallow lakes difficult. Therefore, to encourage a clear condition, the most efficient way to inhibit their expansion and dominance other than manual removal during surveys would be to aerate shallow lakes over the winter period. To combat Eurasian watermilfoil expansion, we should continue to encourage the public to clean their boats and trailers if they enter an infested lake. On the bright side, this invasive helps the lake maintain a clear condition. Overall, more research and surveys should be conducted on shallow lakes to determine the extent of current invasive species' infestation and the effects they have on shallow lake condition stability.

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Tables

Table 1.1. Documented management actions that induced ecosystem shifts in shallow lakes throughout time.

Lake Name	Condition Shifted Towards	Management Action	Year	Source
Christina	Turbid	Dam constructed	1936	Hobbs et al., 2012
	Turbid	Land-clearing and agricultural practices	Post-1950s	Theissen et al., 2012
	Clear	Chemically reduced fish biomass	1965	Hobbs et al., 2012
	Clear	Chemically reduced fish biomass (most planktivores extirpated)	1987	Hobbs et al., 2012
	Clear	Stocking of piscivores	Post-1987	Hobbs et al., 2012
	Clear	Winter refuge aerated for piscivores	1994	Hobbs et al., 2012
	Clear	Chemically reduced fish biomass	2003	Hobbs et al., 2012
Cockshoot Broad	Clear	Dam constructed cutting off sewage-effluent containing river and dredged 70 cm sediment	1982	Moss et al., 1996
	Clear	Fish community manually removed	Winters post-1989	Moss et al., 1996
Krakesjon	Clear	Lowered water level	1800s	Hargeby et al., 2007
Sakylan Pyhajarvi	Clear	Water level drawdowns	1600s, 1850s	Ventela et al., 2016
	Transition	Planktivorous coregonid introduction	Early 1900s	Ventela et al., 2016
	Turbid	Intensified agriculture	Post-1950	Ventela et al., 2016
Shaokatan	Clear	Rehabilition of wetlands, feedlots, and shoreline septic systems	Early 1990’s	MPCA, 2009
Takern	Clear	Lowered water level	1800s	Hargeby et al., 2007
Tamnaren	Clear	Water level drawdown	1870, 1950-54	Wallsten and Forsgren, 1989
	Turbid	Dam Construction	1977	Wallsten and Forsgren, 1989
Veluwe	Turbid	Nutrient loading from agricultural streams and waste-water treatment plants	1960s	Ibelings et al., 2007
	Clear	Winter polder flushing and reduced agricultural catchment nutrient loading	1979	Ibelings et al., 2007
	Clear	Commercial fishery reduced bream stock (~30kg ha^{-1} yr^{-1})	1993-96	Ibelings et al., 2007
	Clear	Zebra Mussels established	1996	Ibelings et al., 2007
	Temporary Turbid	Large-scale dredging	2002	Ibelings et al., 2007
Wolderwijd	Transition to Clear	Polder flushing	Periodically post-1981	Meijer and Hosper, 1997
	Temporary Clear	Biomanipulation (bream and roach) and pike fingerlings stocked	1991	Meijer and Hosper, 1997
Zwemlust	Clear	Biomanipulation	1987-88	Van Donk et al., 1993

Figures

Pre-Industrialization Era (Pre-19th Century)	Industrialization Era (19th-20th Century)	Pollution Control Era (1970's-Present)	Predicted Climate Change Era (2030-2050)
Phytoplankton & Plants			
Phytoplankton communities were stable and vegetation dominated over algal blooms.	Industrialization waste and increased farming produced excess nutrients causing algal blooms.	Reduced nutrient input and aquatic vegetation management reestablished macrophyte colonies.	Warming temperatures increase agal bloom frequency and severity.
Zooplankton			
Zooplankton communities stable with *Daphnia* spp. dominating.	Algal blooms created by waste encourages *Bosmina* spp.	Greater vegetation refuge allows lakes to establish a *Daphnia* spp. dominance.	Warming temperatures create hypoxic conditions causing *Daphnia* spp. to decrease.
Fish			
Optimal habitat for piscivorous species.	Introduction of invasive fish (i.e. Asian Carp) disrupts fish communities and increases bioturbation.	Management of fish community focuses on piscivorous fish dominance.	Warming temperatures are harder for native species to tolerate and shorter winters lead to less fish kills.

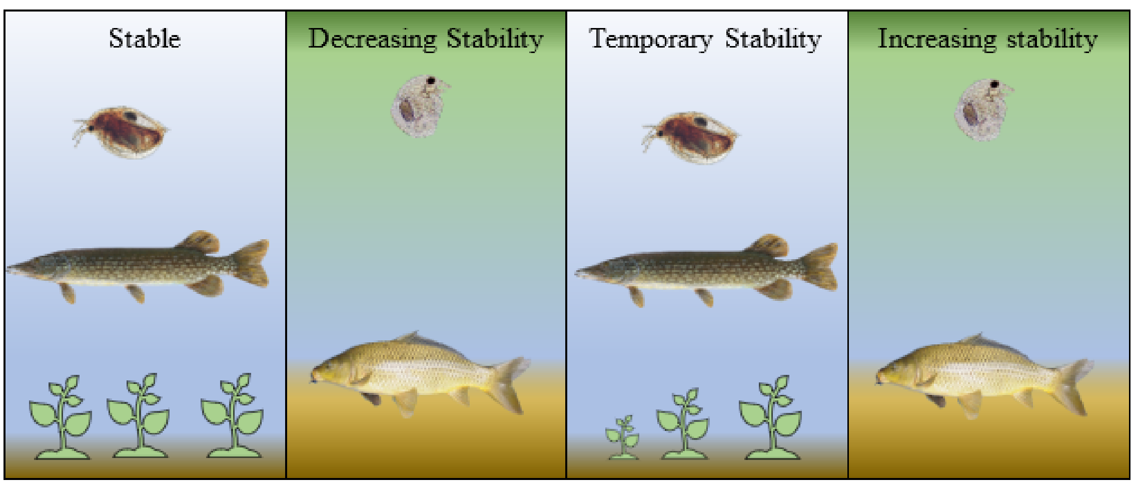

Figure 1.1. Condition and condition stability in shallow lakes through generalized eras. Visual depicts typical phytoplankton/plant prevalence, *Bosmina*/*Daphnia* spp. prevalence, and piscivorous/non-piscivorous fish prevalence. Clear conditions were stable before human disturbance but were less stable during industrialization. Management allowed a somewhat stable clear condition to preside in the Pollution Control Era, but effects of continued climate change will cause turbid conditions to become increasingly stabilized.

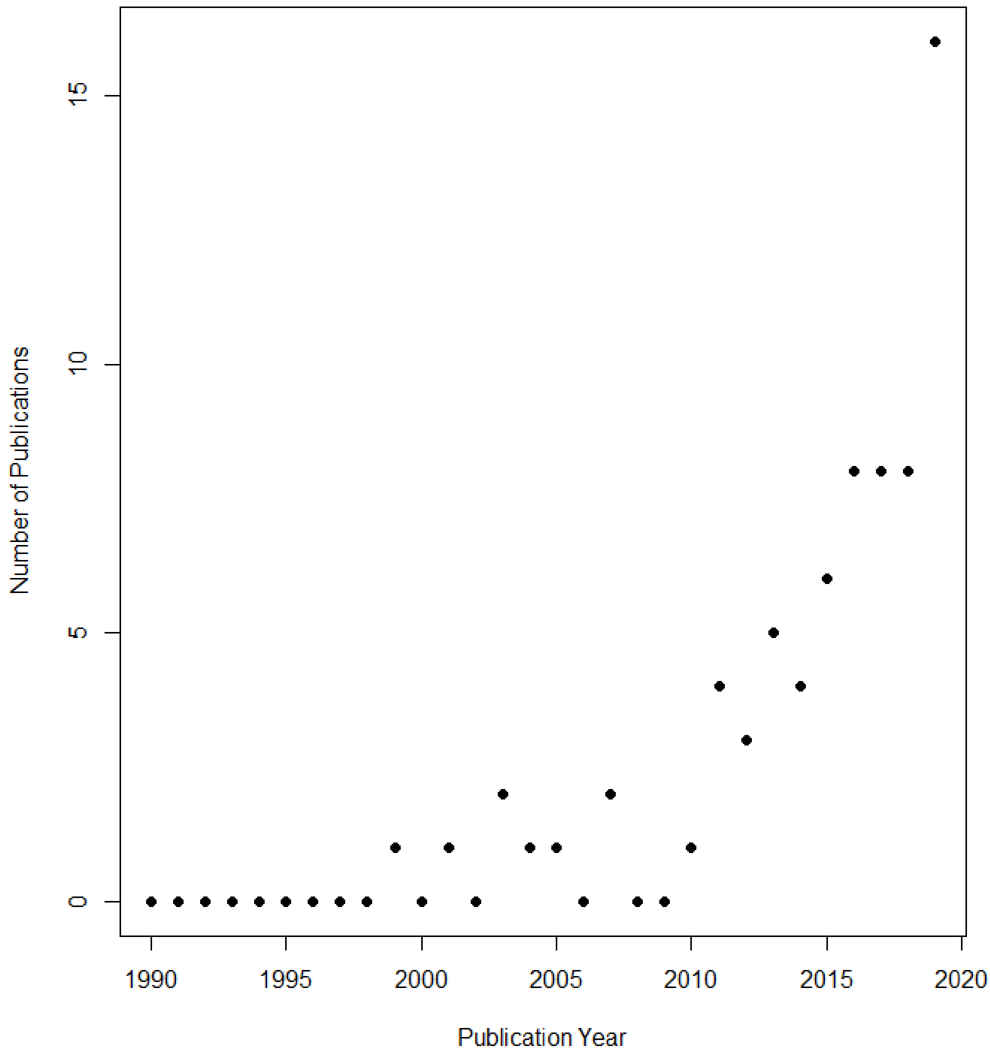

Figure 1.2. Trends in aquatic ecosystem state shift publications from 1990 to 2019 documented through a literature search in Google Scholar with the phrase search of "ecosystem state shifts" containing the exact phrase "state shift".

Chapter 2: Effects of a shallow lake condition shift on habitat, zooplankton, and Yellow Perch dynamics

Abstract- Aquatic ecosystems around the world exist on a continuum between turbid, algal-dominated and clear, macrophyte-dominated conditions, which may influence population dynamics of fish in these systems (such as Yellow Perch *Perca flavescens*). Since turbidity influences the amount of light penetration and occurrence of vegetation, spawning and nursery habitat as well as food availability may change depending on lake condition. For example, a decrease in turbidity encourages a shift in the prevalent zooplankton taxa from *Bosmina* spp. to *Daphnia* spp. We hypothesize many factors associated with a condition shift may combine to influence Yellow Perch, including increased abundance and therefore, intraspecific competition resulting in a reduced length and body condition. We used long-term monitoring data from Lake Shaokatan, Minnesota to examine whether a rarely documented condition shift from a turbid, algal-dominated to a clear, macrophyte-dominated condition occurred in 2014 and whether that shift influenced population dynamics of Yellow Perch, including relative abundance (gillnet CPUE), mean total length (mm), and mean relative weight. A condition shift from turbid to clear was determined in 2014 using mixed effects models that showed significant decreases in phosphorous and chlorophyll-a concentration as well as an increase from a mean of 22% to over 90% vegetation occurrence. The zooplankton community qualitatively showed a prevalence of *Daphnia* spp. and Cyclopoids over small cladocerans during the clear condition period until 2018. Mixed effect models were also used to determine the shift to a clear condition resulted in a significant decrease in Yellow Perch mean total length and relative weight. Therefore, the condition shift and resulting habitat changes that occurred in 2014 and later influenced the size and condition of Yellow Perch. Continued monitoring may overcome variability in relative abundance and help elucidate emerging trends.

Introduction

Aquatic ecosystems exist on a continuum between a turbid, algal-dominated condition and a clear, macrophyte-dominated condition (Scheffer et al. 2001). A condition shift is a term used when an ecosystem shifts between the alternative conditions (Hobbs et. al 2012). Lakes in a clear, macrophyte-dominated condition will tend to have lower nutrient levels, a higher occurrence of macrophytes, and lower abundance of phytoplankton because plants can use nutrients from sediments (Meerhoff and Jeppesen 2009). A lake in a turbid, algal-dominated condition will tend to have cloudy, sediment-filled water and display lower occurrence of macrophytes and higher phytoplankton abundance. These characteristics will then influence zooplankton and fish communities within the system. Shallow lakes are the most abundant lake type worldwide and they are especially vulnerable to cultural eutrophication and condition shifts due to their size (Cael et al. 2016). Although definitions vary, shallow lakes in Minnesota are defined by the Minnesota Department of Natural Resources (MN DNR 2021a) as bodies of water approximately 20 hectares or greater in size and usually 5 meters or less in depth.

Yellow Perch *Perca flavescens* are an important game fish and prey fish for Walleye *Sander vitreus* and other common piscivores found in shallow and other freshwater lakes (Sheppard et al. 2015; Pothoven et al. 2016). Variable growth rates among Yellow Perch populations have been explained by abiotic factors like lake productivity (Uphoff and Schoenebeck 2012) and biotic factors like intra- and inter-specific competition (Schoenebeck and Brown 2010; Kaemingk et al. 2012; Munter et al. 2019). Similarly, Yellow Perch recruitment has been impacted by abiotic and biotic factors (Kaemingk et al. 2014; Dembkowski et al. 2017; Munter et al. 2019). Therefore, it is logical that Yellow Perch and other piscivores are affected by condition shifts.

Condition shifts have the potential to influence Yellow Perch whether they are induced by bottom-up or top-down mechanisms. Bottom-up cascades may begin with an increase in phosphorous concentration (i.e., carried in runoff water or introduced through decaying matter) or removal of sediment-stabilizing aquatic vegetation (i.e., resuspension of sediment and attached phosphorous particles). Both events increase the phosphorous concentration in the water column and encourage higher occurrence of algal blooms and greater *Bosmina* spp. biomass rather than aquatic vegetation and *Daphnia* spp. due to algae using dissolved phosphorous more readily and *Bosmina* spp. having a specialized foraging mode (Brothers et al. 2013; DeMott and Kerfoot 1982). Yellow Perch consume *Daphnia* spp. at an early age (Prout et al. 1990; Liao et al. 2002) and sometimes adult Yellow Perch still consume zooplankton along with small-bodied fish species, including smaller Yellow Perch (Lott et al. 1996, 1998; Liao et al. 2004; Munter et al. 2019). Therefore, a decrease in *Daphnia* spp. abundance may result in a disadvantage for piscivores (i.e., Yellow Perch) and an advantage for non-piscivores (i.e., Bullhead *Ameirus* spp.). Non-piscivores such as Bullhead are often removed to prevent uprooting of vegetation and sediment disturbance (Garcia-Berthou 2001), protecting habitat for Yellow Perch and other piscivores that play a key role in recruitment (Massicote et al. 2015). As fish abundance (i.e., Yellow Perch) increases, competition for prey items and optimal habitat can lead to slowing growth often observed as decreased mean length and relative weight (Heath and Roff 1996; Schoenebeck and Brown 2010; Kaemingk et al. 2012; Munter et al. 2019).

The Lake Shaokatan watershed in Southwest Minnesota, USA (3,661 hectares), underwent purposeful land-use changes in the early 1990's to encourage wildlife habitat and boost the Walleye fishery within shallow Lake Shaokatan. Lake Shaokatan (407 hectares surface area) is a shallow (3.0 m max depth, 2.4 m mean depth) polymictic prairie lake. Through rehabilitation of three wetland areas, four animal feedlots, and shoreline septic system improvements, the lake was removed from the impaired waters list after water quality standards were met in 2014-2015 (MPCA 2009). Total phosphorous decreased from >75 µg/L in 2013 to 33 µg/L in 2014 and algal biomass was also lower in 2014 consisting of prominent cryptophytes and diatoms rather than blue-green algae (Heiskary et al. 2016). Corresponding with the phosphorous concentration thresholds of 50 µg/L or lower to be classified as a lake in a clear condition, identified by Vitense et al. (2018), we hypothesize this shallow lake shifted to a clear condition in 2014. This is a unique opportunity to study a rarely documented shift from a turbid to a clear condition in a shallow lake and the resultant effects on habitat, prey, and fish populations. The objectives of this study are: (1) determine whether a condition shift occurred (via changes in concentrations of phosphorous and chlorophyll-a, Secchi depth, and/or vegetation occurrence) and if so, (2) examine how a condition shift influenced Yellow Perch population dynamics (via changes in habitat and prey). These findings aim to expand current knowledge of effects of condition shifts on Yellow Perch in shallow lakes.

Methods

Water quality characteristics

Data were collected through the Sentinel Lakes Program (MN DNR 2021a), which is a collaborative, long-term monitoring effort between MN DNR and the Minnesota Pollution Control Agency (MPCA). Total phosphorous was collected monthly (bi-weekly when possible) by the MPCA at a single site before 9 am in open-water months (April through November) according to water quality assessment standards (MPCA 2016). Secchi depth measurements were taken by lowering a Secchi disk into the water until it disappeared, following the aforementioned time frame.

Plants

The MN DNR annually surveyed plants on Lake Shaokatan using the lake-wide point intercept survey method (MN DNR 2016b) to estimate percent of the littoral zone containing vegetation. Surveyors navigated to within 5 m of predetermined sites, ranging from 77-347 sites throughout the study period, using GPS units on boats without anchoring. In the depth zone from shore to 1.5 m, sites were spaced 65 m apart, while those in greater depths were spaced 195 m apart. These were chosen based on required number of sample sites within each zone to reliably estimate frequencies initially determined using the formula produced by Newman et al. (1998). Sampling at a location consisted of an approximated square meter off a designated side of the boat. Plant presence was noted as present or not present at each site through visual cues and with a single rake sampler toss. Percent frequency of occurrence was then calculated by dividing the number of sites with vegetation present by the total number of sites and multiplying by 100.

Phytoplankton

The MPCA annually collected phytoplankton samples once a month from May through October at the surface of the lake’s site of maximum depth using a 2 m polyvinyl chloride (PVC) integrated tube with a diameter of approximately 3 cm (MN DNR 2016a). Samples were stored on ice and in the absence of light until they were decanted into a dark plastic bottle (250 mL) and preserved with Lugol’s Solution (glutaraldehyde post-2017 due to preservation preference) for later analysis. In the lab, the water sample was homogenized by shaking 100 times before a calibrated Eppendorf micropipette transferred a 0.02 L sample to a cuvette. Chlorophyll *a* concentration was calculated with a correction for pheophytin, according to standard methods (APHA 1980) and represented the relative biomass of phytoplankton within the sample. These values were averaged across all months each year.

Zooplankton

The MPCA collected zooplankton samples by a monthly vertical tow from May to October using a 30 cm mouth, 80 µm mesh simple zooplankton net (MN DNR 2016a). Each net was set within 0.5 m of the bottom and hauled approximately 0.5 meter per second. The net was then rinsed into sample bottles topped with 100% reagent alcohol and later analyzed by the MN DNR. Each sample was adjusted to a known volume by rinsing specimens into a graduated beaker from an 80 µm mesh net and adding water to a volume that provided 150 organisms or more per 5 mL aliquot. A 5 mL aliquot was withdrawn using a bulb pipette and transferred to a counting wheel for each sample. Organisms were identified by species, counted, and measured to within 0.01 mL using a dissecting microscope and an image analysis system. Biomass estimates (µg/L) for each taxonomic group were calculated using length-weight regression coefficients based on dry weight, obtained from Culver et al. (1985) and Dumont et al. (1975). These values were summed then averaged across all months to provide a single value for annual group biomass comparisons. Percent composition was calculated by dividing each monthly biomass by its unique total biomass and multiplying by 100 for each group, then averaging for an annual percent composition. Zooplankton samples were qualitatively compared as there is one year of pre-shift data.

Fish

The MN DNR sampled Yellow Perch populations using experimental, multifilament gill nets 76.2 m long and 1.5 m deep, divided into five 15.2 m panels of 19, 25, 31, 38, and 50 mm bar mesh according to a standardized lake survey protocol (MN DNR 1993). Typically, three gill nets were fished overnight at three of six predetermined site locations on the first week of August. Captured fish (separated by mesh size) were identified, counted, measured for total length (TL, mm), and weighed (g). Aging structures (otoliths) were taken from Yellow Perch (10/cm group) and ages estimated. Otoliths from age-1 fish were read whole (2009, 2014) while older group ages were estimated using the crack and burn method, sanding the halves and using mineral oil to smooth the surface for readings (2018). Length at age data was not analyzed due to limited repetitions but is included in Table 2.3 as additional qualitative information. Relative weight (Wr) for each fish was calculated using weight divided by the standard weight and multiplied by 100 (Wege and Anderson 1978). Standard weight values were found using the published standard weight equation intercept and slope values for Yellow Perch (Willis et al. 1991). Proportional Size Distribution (PSD, formerly Proportional Stock Density, Guy et al. 2007) was calculated through dividing the number of Yellow Perch at ≥ 200 mm (minimum quality length) by the number of Yellow Perch ≥ 130 mm (minimum stock length) and multiplied by 100 (Willis et al. 1993).

Statistical analyses

Models were used to determine if statistical differences occurred in the habitat and fish variables pre- and post-2014. Fitted random-coefficient mixed-effects models were used to account for repeated measures and unequal sampling intervals (Bethke and Staples 2015) with significance determined as $|t| \geq 2$ (Linck and Cunnings 2015; Luke 2017). To determine evidence of a shift 2014 and later, habitat variables of phosphorous, Secchi depth, and chlorophyll-a concentration were tested as a response to the condition shift and month as fixed effects with year as a random effect. For example, P~RegShift + Month + (1|Year), with RegShift grouping pre-2014 years against 2014 and later years. Fish methods of CPUE, TL, and Wr were tested as a response to the condition shift as a fixed effect with year as a random effect. For example, Wr~RegShift + (1|Year). Mean CPUE of Yellow Perch was log transformed for analysis to achieve normality and due to CPUE values of 0 in 2004, a detection limit for zeroes was used. The detection limit was calculated by the minimum detectable CPUE halved with the minimum detection calculated as mean from Poisson distribution with 80% probability of CPUE ≥1 (Clarke 1998). PSD was qualitatively compared due to singular annual estimates leading to only 3 post-2014 values.

Results

Habitat

Long-term monitoring resulted in a robust habitat dataset, amounting to 14 annual phosphorous samples, 20 annual Secchi depth samples, 16 annual chlorophyll-a samples, and 10 annual plant surveys (Table 2.1). Mean phosphorous concentrations significantly decreased after 2014 by 90.4 μ/L (SE=11.6, t=-7.824, $P<0.001$). Secchi depth was not significantly different after 2014 (t=1.918, $P=0.64$), however, the greatest mean Secchi depths correlated with the years of low phosphorous concentrations (2015-2017). Mean chlorophyll-a concentration significantly decreased by 33.6 μ/L (SE=11.9, t=-2.830, $P<0.001$), and were especially low during 2014-2017. Plant occurrence was greatest 2015-2017 where it stabilized over 90% (Table 2.1). These results overall coincide to support the classification of a clear condition beginning in 2014 and later (Figure 2.1).

Zooplankton prey source

Annual zooplankton community samples were taken seven consecutive years (see Table 2.2) and are hereafter qualitatively compared. Total zooplankton biomass was highest in 2013 and was mainly comprised of large *Daphnia* spp. Biomass of Calanoid copepods seem to be higher in 2014, while 2015-2017 had higher biomass of Cyclopoid copepods. Post-2017 community samples show the biomass of small cladocerans may have been greater than the biomass of large *Daphnia* spp., coinciding with a decrease in Secchi depth (Figure 2.2).

Yellow Perch

Fish were surveyed in 10 years over the course of the study period with 1,817 Yellow Perch sampled. Mean Yellow Perch CPUE ranged from 1 to 148, Wr ranged from 97 to 115, TL ranged from 171 to 252 mm, and PSD ranged from 1 to 100 (Table 2.3). Yellow Perch CPUE did not significantly differ after the condition shift of 2014 (t=1.291, $P=0.89$). Yellow Perch Wr significantly decreased by 9 (SE=2.3) after 2014 (t=-3.784, $P=0.002$). Wr was consistently above 100 until the shift in 2014 and was lowest in the year 2018. Yellow Perch Wr was inversely correlated to percent occurrence of vegetation ($P=0.005$) but was not explained by CPUE ($P=0.32$, Figure 2.3). TL significantly decreased by 37 mm (SE=12.4) after 2014 (t=-2.943, $P=0.007$) and the two lowest mean lengths occurred post-shift to clear water conditions. Finally, PSD did not qualitatively show a clear trend between the two conditions. In summary, Yellow Perch displayed a significant decrease in Wr and TL after the shift in 2014 to a clear, macrophyte-dominated condition.

Discussion

A key outcome of this study is that a shift from a turbid, algal-dominated condition to a clear, macrophyte-dominated condition influenced fish population dynamics (via total length and relative condition) in these systems (i.e., Yellow Perch). Phosphorous and chlorophyll-a concentrations along with aquatic plant occurrence displayed significant changes in 2014 and later. In accordance with phosphorous thresholds of 50 µg/L as suggested by Vitense et al. (2018), the lake has entered a clear condition in 2014. Similar to previous studies, Lake Shaokatan displayed lower nutrient levels, a higher abundance of macrophytes, and lower phytoplankton abundance indicative of a clear water condition (McGowan et al. 2005; Meerhoff and Jeppesen 2009; Hobbs et al. 2012). Although post-2014 was the only period that a Secchi depth of ≥2 m was achieved, it was most likely not significant due to the lower values in the last two data years. Although there are not currently enough years to properly test it, 2018 and 2019 showed a slight increase in phosphorous and a decrease in Secchi depth and vegetation. It is important to continue monitoring this lake to better understand the stability and duration of condition shifts as a shift back towards a turbid condition could occur. However, the decrease in phosphorous concentration and chlorophyll-a concentration paired with an increase in vegetation occurrence seen in 2014-2017 follows the expected trend of clear water conditions and therefore, the lake condition is classified as clear. Although beyond the scope of this study, this shift can likely be attributed to the land-use changes implemented in the 1990's (MPCA 2009).

The qualitative observations of zooplankton community structure and greater biomass of large *Daphnia* spp. compared to small cladocerans during 2015-2017 is also supportive evidence of this documented condition shift. Without knowing what the community looked like prior to 2013, it is possible (speculated due to no vegetation or phosphorous data that year) that 2013 had enough reduction in turbidity to encourage greater *Daphnia* spp. biomass and the lag in Yellow Perch abundance response offered predation release for the large-bodied cladoceran. Havens et al. (2007) also found a zooplankton community significantly changed, specifically by a loss of dominant cladocerans, after a drought period that encouraged rapid development of submerged vegetation in a shallow lake. This is a plausible explanation for the high *Daphnia* spp. abundance and total zooplankton biomass observed in Lake Shaokatan during 2013 as a drought occurred 2012-2013, during which the lake dropped by over 20% in water level (MN DNR 2021b). These drought conditions may have increased turbidity and chlorophyll-a due to shorter water column mixing and nutrient resuspension, which may explain the observed increases in chlorophyll-a and greater biomass of zooplankton and prevalence of *Daphnia* spp. in 2013, particularly (Olds et al. 2011; Olds et al. 2014). The increase in phosphorous and chlorophyll-a concentration after 2017 coincided with a qualitatively observed increase in small cladocerans biomass (primarily *Bosmina* spp.), which can be explained by *Bosmina* spp. having greater density and reproductive rates over *Daphnia* spp. when phosphorous addition occurs in a system (DeMott and Kerfoot 1982). Therefore, the observed prevalence of *Daphnia* spp. during 2015-2017 support the clear condition classification, but further monitoring should be continued to determine whether the rise in *Bosmina* spp. is indicative of a shift towards a turbid condition after 2017.

Yellow Perch population dynamics changed significantly in response to a shift from a turbid to a clear condition. Perch caught 2014 and later were significantly shorter and in poorer condition. The increase in water clarity after the lake's shift to a clear condition in 2014 allowed vegetation occurrence in over 90% of the lake, which may have provided Yellow Perch refuge from predation pressure by Walleye and other piscivores, potentially increasing Yellow Perch abundance and intraspecific competition for resources. Yellow Perch Wr was negatively correlated to vegetation occurrence in which the years containing higher occurrence of vegetation displayed a lower Wr. A decrease in preferred zooplankton prey post-condition shift may also further contribute to intraspecific competition. For example, Cyclopoid copepods became more prevalent and are known to be less susceptible to visual predators than cladocerans (Williamson et al. 2020). The lowest Yellow Perch Wr and TL recorded (2018) corresponded to an observed switch in the zooplankton community from *Daphnia* spp. (a large, preferred zooplankton prey) to *Bosmina* spp. (a smaller, not advantageous prey). Although interspecific competition has been found to impact Yellow Perch growth in other systems (Schoenebeck and Brown 2010; Munter et al. 2019), low abundance of Bluegill *Lepomis macrochirus* in Lake Shaokatan (only 1 Bluegill sampled) suggests this is not as likely of a hypothesis for observed changes in Yellow Perch population dynamics as intraspecific competition.

Yellow Perch length and condition significantly decreased following the shift to a clear condition, while our hypothesis that relative abundance would increase was not statistically supported. Natural variability in Yellow Perch year-class strength (Uphoff and Schoenebeck 2012; Munter et al. 2019), especially during the turbid condition, and variable sampling efficiency may have increased variation in CPUE, rendering this comparison statistically not significant between conditions. Abundant vegetation in 2014 and later may have impeded Yellow Perch from capture as it has been shown that CPUE can be affected by and have greater variability due to dense vegetation when using standard gillnets (Portt et al. 2006).

In summary, this study examined a rarely documented shift from a turbid, algal-dominated condition to a clear, macrophyte-dominated condition beginning in 2014 in a Minnesota shallow lake by documenting changes at multiple trophic levels related to Yellow Perch habitat, prey, and population dynamics. The robust habitat dataset followed expected trends as phosphorous concentrations and chlorophyll-a concentrations decreased, allowing greater water clarity (Secchi depth) and consistent vegetation occurrence. Zooplankton communities also followed expected trends as large *Daphnia* spp. had a larger biomass compared to small cladocerans during the clear condition. Aided by the amount of vegetation providing refugia during the clear water condition, Yellow Perch population dynamics were characterized by smaller Yellow Perch with a lower Wr that may have been due to intraspecific competition. This study would not be possible without the long-term monitoring data collected by the MN DNR and MPCA as part of the Sentinel Lakes Program. Therefore, future research should mimic this study by using long-term datasets for multiple trophic levels to investigate the large picture of condition shifts in aquatic ecosystems. Documenting changes in each trophic level in a shallow lake with a detailed long-term dataset is key to understanding the condition shift as a whole.

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Tables

Table 2.1. Habitat characteristics of Lake Shaokatan, Lincoln County, MN observed in 2000-2019. Phosphorous concentration, Secchi depth, and chlorophyll-a concentrations (corrected for pheophytin) sampled April-November are shown as yearly averages with standard deviation in parentheses. Vegetation occurrence is percent of lake-wide intercept survey sites with plants present annually.

Year	P conc. (µg/L)	Secchi Depth (m)	Chl-a (µg/L)	Vegetation Occurrence
2000	154 (77)	1.4 (0.6)	36.63 (36.37)	19.72
2001	168 (90)	1.0 (0.5)	99.33 (69.23)	-
2002	124 (31)	1.4 (0.8)	55.10 (56.10)	2.5
2003	182 (32)	0.8 (0.2)	22.32 (20.85)	-
2004	-	1.6 (0.9)	-	-
2005	152 (100)	1.9 (0.9)	47.97 (57.48)	-
2006	-	1.8 (0.9)	-	-
2007	-	1.5 (0.8)	-	-
2008	134 (42)	1.0 (0.8)	68.39 (56.82)	23.63
2009	-	1.3 (0.8)	10.11 (8.48)	21.74
2010	79 (7)	1.2 (0.8)	29.59 (42.28)	33.14
2011	99 (29)	1.7 (0.6)	15.92 (15.62)	32.66
2012	-	1.5 (0.6)	-	-
2013	-	1.9 (0.9)	65.70 (86.42)	-
2014	31 (12)	2.0 (0.6)	7.19 (5.47)	-
2015	60 (67)	2.5 (0.5)	7.51 (8.62)	97.62
2016	59 (37)	2.4 (0.7)	7.75 (5.32)	95.14
2017	24 (4)	2.4 (0.4)	6.29 (3.82)	93.31
2018	77 (24)	0.8 (0.3)	21.48 (8.00)	77.85
2019	77 (48)	1.3 (0.8)	33.02 (32.94)	-

Table 2.2. Zooplankton biomass from Lake Shaokatan, Lincoln County, MN observed in 2013-2019. Total biomass, Calanoid biomass, Cyclopoid biomass, Large *Daphnia* spp. biomass, small Cladocera biomass, percent composition Large *Daphnia* spp., and percent composition small cladoceran sampled May-October are shown as yearly averages with standard deviation in parentheses.

	Average Biomass (μg/L)						
Year	Total	Calanoid	Cyclopoid	Large Daphnia	Small Cladocera	% Daphnia	% Sm Cla
2013	1110 (1279)	106 (76)	48 (28)	913 (1249)	33 (43)	55 (31)	2 (2)
2014	397 (144)	240 (99)	60 (50)	31 (36)	53 (61)	8 (12)	14 (15)
2015	136 (141)	12 (29)	51 (54)	41 (100)	14 (14)	11 (26)	20 (16)
2016	216 (236)	1 (2)	142 (203)	33 (81)	28 (37)	15 (37)	12 (15)
2017	166 (208)	1 (2)	66 (104)	57 (97)	17 (12)	17 (26)	27 (25)
2018	350 (307)	10 (11)	122 (190)	7 (17)	188 (183)	6 (12)	51 (33)
2019	590 (443)	71 (72)	173 (297)	62 (113)	232 (368)	10 (20)	46 (38)

Table 2.3. Yellow Perch population dynamics from Lake Shaokatan, Lincoln County, MN observed in July/August of 1996-2018. All values (excluding N and PSD) are shown as the annual mean and standard deviations are in parentheses. Total Yellow Perch individuals annually caught in gillnets are represented by N. Relative weight for Yellow Perch was calculated using intercept and slope values from Willis et al. (1991) and proportional size distribution was calculated using stock and quality values in Willis et al. (1993). Mean length at age (LAA) was an average of observed lengths at specified ages.

Year	N	CPUE	Relative Weight (Wr)	Total Length (mm)	LAA 1 (mm)	LAA 3 (mm)	PSD
1996	96	24 (9)	107 (6)	202 (20)	-	-	47
2000	443	148 (16)	105 (7)	232 (13)	-	-	99
2004	2	1 (1)	-	-	-	-	-
2008	116	39 (12)	107 (7)	218 (37)	-	-	58
2009	58	19 (4)	115 (9)	205 (52)	175 (12)	284 (28)	28
2010	226	75 (18)	102 (10)	191 (29)	-	197 (13)	28
2011	65	22 (12)	110 (8)	252 (22)	-	-	100
2014	130	43 (11)	100 (9)	173 (15)	170 (16)	-	1
2015	240	80 (60)	99 (12)	199 (34)	-	-	66
2018	441	147 (84)	97 (8)	171 (21)	-	178 (17)	9

Figures

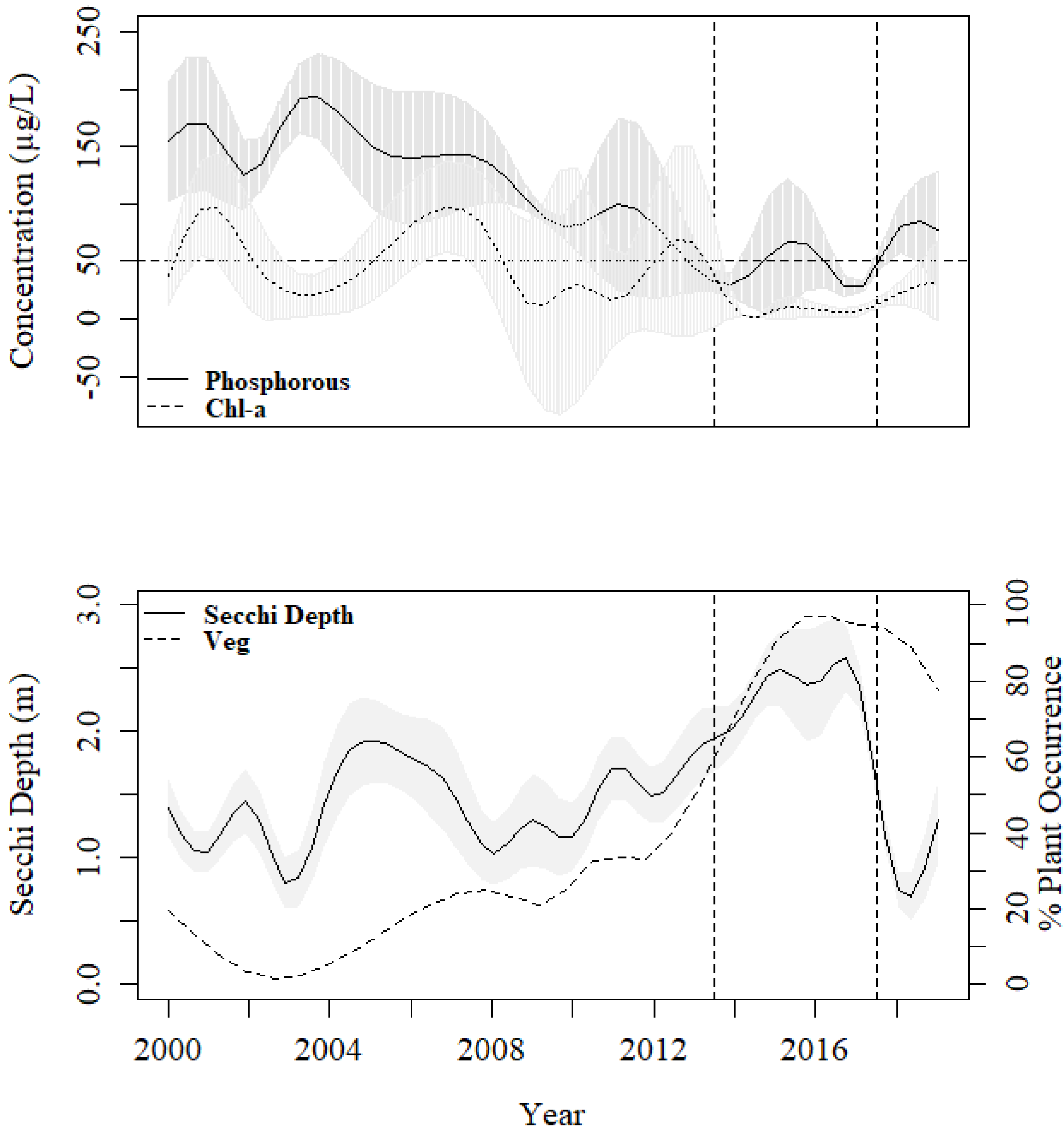

Figure 2.1. Annual averages of total phosphorous and chlorophyll-a concentration (µ/L) collected April-November, Secchi depth (m) collected May-October, and percent vegetation occurrence in August from 2000 to 2019 in Lake Shaokatan, Lincoln County, MN. Shaded regions represent 95% confidence intervals. Dashed black line prior to 2014 represents condition shift from turbid to clear condition based on thresholds (shown by horizontal dashed line) determined by Vitense et al. (2018). Dotted black line prior to 2018 represents a potential shift to be further monitored.

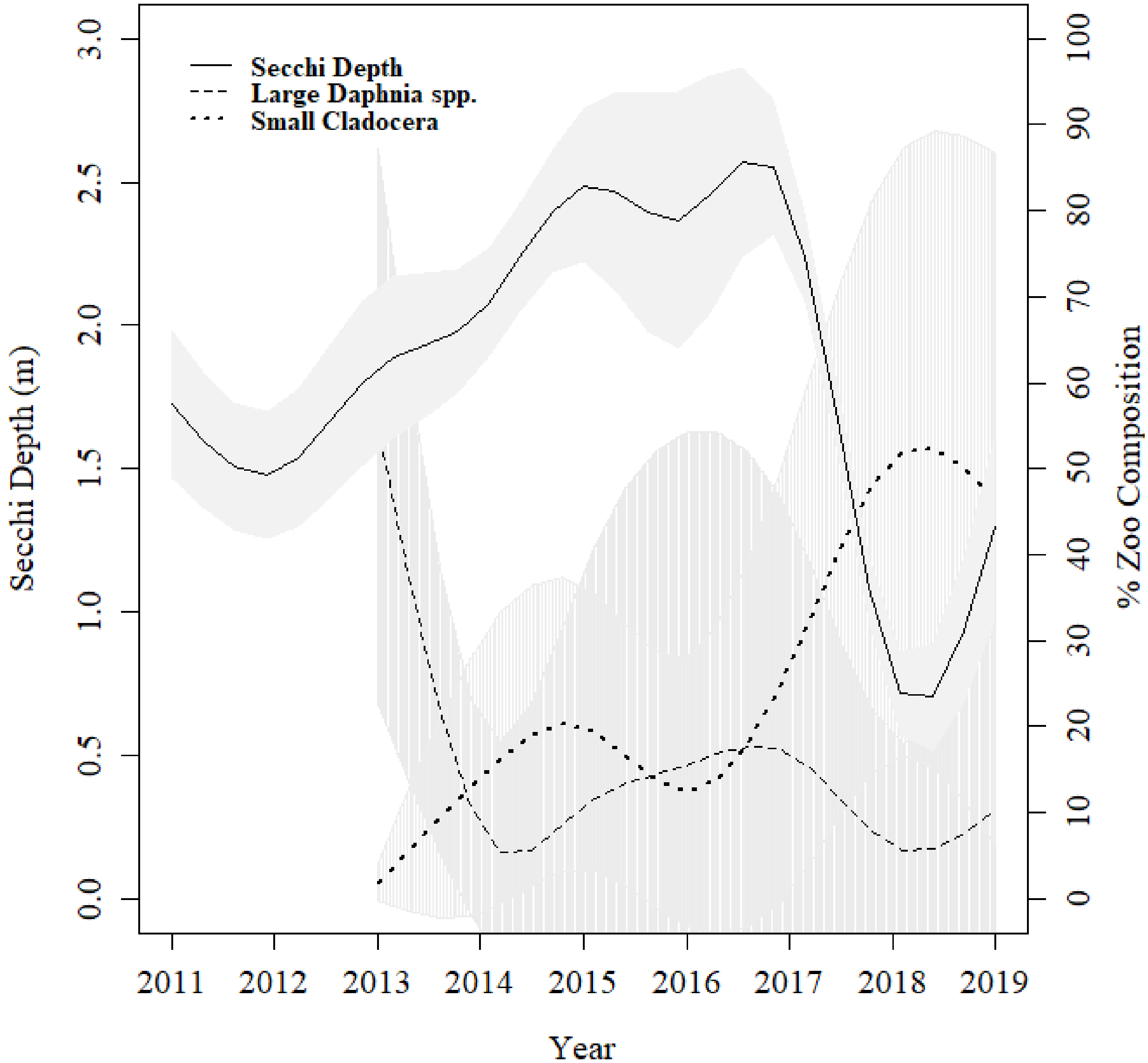

Figure 2.2. Annual average Secchi depth (m) and percent composition of large *Daphnia* spp. and small cladocera of zooplankton community collected May-October in Lake Shaokatan, Lincoln County, MN throughout 2011-2019. Shaded regions represent 95% confidence intervals.

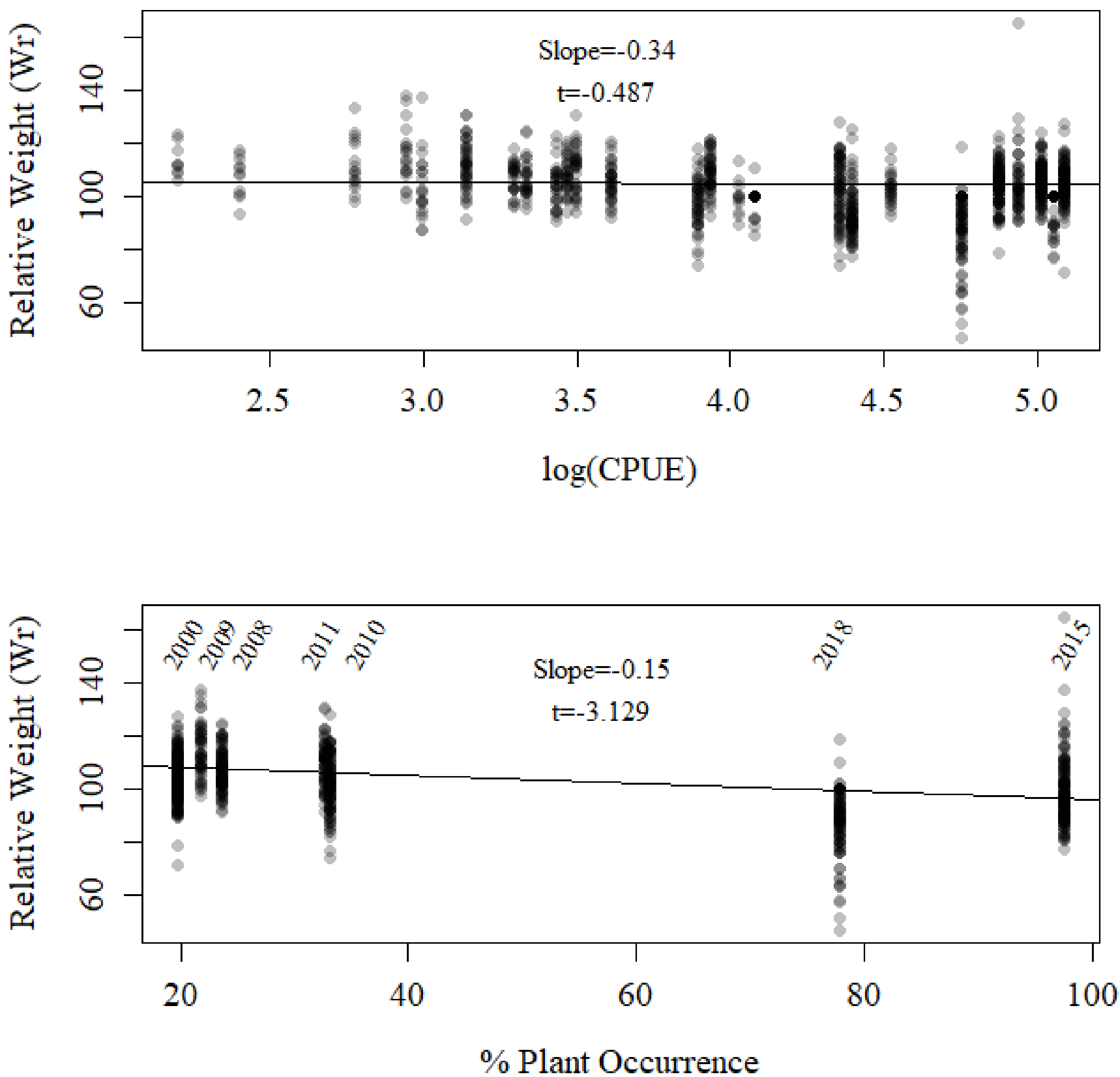

Figure 2.3. Yellow Perch relative weight (Wr) linear regression with log-transformed gillnet catch per unit effort (CPUE; top) and percent plant occurrence (bottom) collected August in Lake Shaokatan, Lincoln County, MN throughout 1996-2019. Random-coefficient mixed effects models were used with t ≥ |2| being significant (i.e., Wr~Veg+(1|Year)). As vegetation occurrence increases, the relative weight of individual fish decreases significantly. CPUE did not show a significant relationship with relative weight.