

SPECIAL SECTION: EFFECTS OF ECOSYSTEM CHANGE ON NORTH AMERICAN PERCID POPULATIONS

Effects of a Shallow Lake Condition Shift on Habitat, Zooplankton, and Yellow Perch Dynamics

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Abstract

Aquatic ecosystems around the world exist on a continuum between turbid, algal-dominated conditions 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 hypothesized that many factors associated with a condition shift may combine to influence Yellow Perch, including increased abundance and therefore increased 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 condition to a clear, macrophyte-dominated condition occurred in 2014 and whether that shift influenced population dynamics of Yellow Perch, including relative abundance (gill-net CPUE), mean total length, and mean relative weight. A condition shift from turbid to clear was determined in 2014 using mixed-effects models that showed significant decreases in phosphorus 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 that 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.

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

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 Received March 3, 2021; accepted October 12, 2021

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) as bodies of water approximately 20 ha or greater in size and usually 5 m or less in depth (MN DNR 2021a).

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 interspecific 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 (DeMott and Kerfoot 1982; Brothers et al. 2013). 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 nonpiscivores (i.e., Bullhead *Ameiurus* spp.). Nonpiscivores 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, which is 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 southwestern Minnesota (3,661 ha) underwent purposeful land-use changes in the early 1990s to encourage wildlife habitat and boost the Walleye fishery within shallow Lake Shaokatan. Lake Shaokatan (407-ha surface area) is a shallow (3.0-m maximum depth, 2.4-m mean depth) polymictic prairie lake. Through rehabilitation of three wetland areas and 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 threshold of 50 µg/L or lower that is needed for a lake to be classified as in a clear condition, as identified by Vitense et al. (2018), we hypothesize that 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 were (1) to 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 the 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 (biweekly when possible) by the MPCA at a single site before 0900 hours 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 lakewide point intercept survey method (MN DNR 2016a) to estimate percent of the littoral zone containing vegetation. Surveyors navigated to within 5 m of predetermined sites, ranging from 77 to 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 the 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 PVC integrated tube with a diameter of approximately 3 cm (MN DNR 2016b). 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 was used after 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- μ m-mesh simple zooplankton net (MN DNR 2016b). Each net was set within 0.5 m of the bottom and hauled at approximately 0.5 m/s. The net was then rinsed into sample bottles topped with 100% reagent alcohol and was later analyzed by the MN DNR. Each sample was adjusted to a known volume by rinsing specimens into a graduated beaker from an 80- μ m-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 (μ g/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 preshift data.

Fish.—The MN DNR sampled Yellow Perch populations using experimental, multifilament gill nets that were 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 (mm), and weighed (g). Aging structures (otoliths) were taken from Yellow Perch (10 per length-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 were not analyzed due to limited repetitions. Relative weight 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 (formerly proportional stock density; Guy et al. 2007) was calculated through dividing the number of Yellow Perch ≥ 200 mm (minimum quality length) by the number of Yellow Perch ≥ 130 mm (minimum stock length) and multiplying by 100 (Willis et al. 1993).

Statistical analyses.—Models were used to determine if statistical differences occurred in the habitat and fish variables before and after 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 in 2014 and later, habitat variables of phosphorous, Secchi depth, and chlorophyll *a* concentration were tested as a response to the condition shift, with month as a fixed effect and year as a random effect. For example, $P \sim \text{RegShift} + \text{month} + (1|\text{year})$, with RegShift grouping pre-2014 years against 2014 and later years. Fish measurements of CPUE, total length, and relative weight (Wr) were tested as a response to the condition shift as a fixed effect with year as a random effect. For example, $\text{Wr} \sim \text{RegShift} + (1|\text{year})$. Mean CPUE of Yellow Perch was log transformed for analysis to achieve normality, and due to CPUE values of zero 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). Proportional size distribution was qualitatively compared due to singular annual estimates leading to only three post-2014 values.

RESULTS

Habitat

Long-term monitoring resulted in a robust habitat data set, amounting to 14 annual phosphorous samples, 20

annual Secchi depth samples, 16 annual chlorophyll *a* samples, and 10 annual plant surveys (Table 1). Mean phosphorous concentrations significantly decreased after 2014 by 90.4 µg/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* concentrations significantly decreased by 33.6 µg/L (SE = 11.9; $t = -2.830$, $P < 0.001$) and were especially low during 2014–2017. Plant occurrence was greatest from 2015 to 2017, during which it stabilized over 90% (Table 1). These results overall coincide to support the classification of a clear condition beginning in 2014 and later (Figure 1).

Zooplankton Prey Source

Annual zooplankton community samples were taken seven consecutive years (see Table 2) and are hereafter qualitatively compared. Total zooplankton biomass was highest in 2013 and was mainly comprised of large *Daphnia* spp. The biomass of calanoid copepods seems to be higher in 2014, while 2015–2017 had a higher biomass of cyclopoid copepods. Post-2017 community samples show that 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).

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, relative weight ranged from 97 to 115, total length ranged from 171 to 252 mm, and proportional size distribution ranged from 1 to 100 (Table 3). Length-at-age data were not analyzed due to limited repetitions but are included in Table 3 as additional qualitative information. Yellow Perch CPUE did not significantly differ after the condition shift of 2014 ($t = 1.291$, $P = 0.89$). Yellow Perch relative weight significantly decreased by 9 (SE = 2.3) after 2014 ($t = -3.784$, $P = 0.002$). Relative weight was consistently above 100 until the shift in 2014 and was lowest in the year 2018. Yellow Perch relative weight was inversely correlated to percent occurrence of vegetation ($P = 0.005$) but was not explained by CPUE ($P = 0.32$; Figure 3). Total length significantly decreased by 37 mm (SE = 12.4) after 2014 ($t = -2.943$, $P = 0.007$), and the two lowest mean lengths occurred after the shift to clear water conditions. Finally, proportional size distribution did not qualitatively show a clear trend between the two conditions. In summary, Yellow Perch displayed a significant decrease in relative weight and total length after the shift in 2014 to a clear, macrophyte-dominated condition.

TABLE 1. Habitat characteristics of Lake Shaokatan, Lincoln County, Minnesota, 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 deviations in parentheses. Vegetation occurrence is the percent of lakewide intercept survey sites with plants present annually.

Year	Phosphorous concentration (µg/L)	Secchi depth (m)	Chlorophyll <i>a</i> (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)	

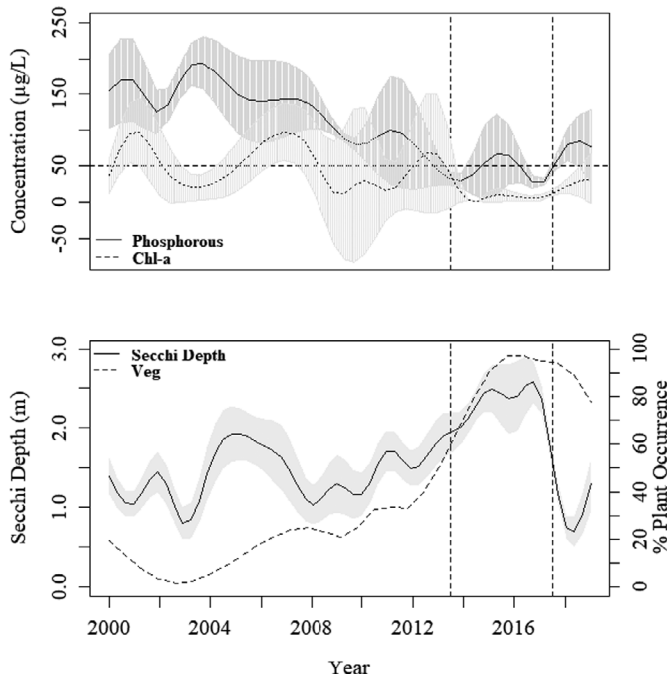


FIGURE 1. Annual averages of total phosphorous and chlorophyll *a* concentration ($\mu\text{g/L}$) collected April–November, Secchi depth (m) collected May–October, and percent vegetation occurrence in August from 2000 to 2019 in Lake Shaokatan, Lincoln County, Minnesota. Shaded regions represent 95% confidence intervals. The vertical dashed black line prior to 2014 represents the condition shift from turbid to clear condition based on thresholds (shown by horizontal dashed line in top panel) determined by Vitense et al. (2018). The vertical dashed black line prior to 2018 represents a potential shift to be further monitored.

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

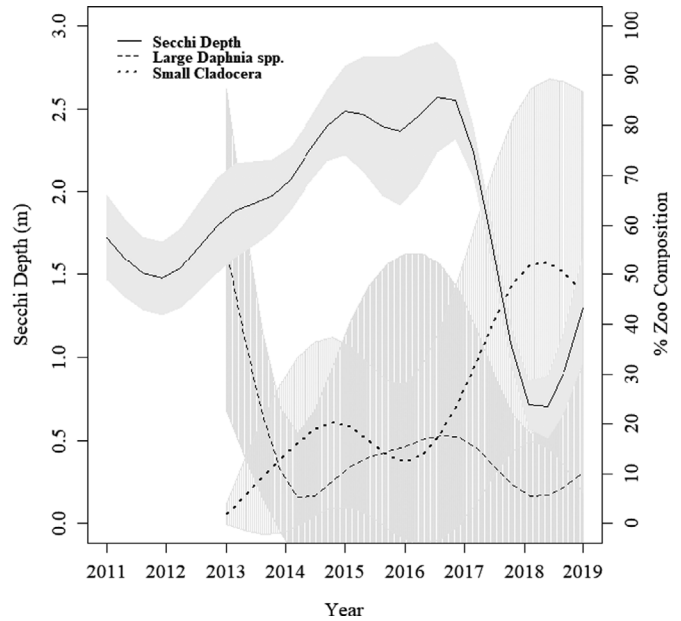


FIGURE 2. Annual average Secchi depth (m) and percent composition of large *Daphnia* spp. and small cladocerans in the zooplankton community collected May–October in Lake Shaokatan, Minnesota, throughout 2011–2019. Shaded regions represent 95% confidence intervals.

significant changes in 2014 and later. In accordance with phosphorous thresholds of $50 \mu\text{g/L}$ as suggested by Vitense et al. (2018), the lake 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 Jepsen 2009; Hobbs et al. 2012). Although after 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

TABLE 2. Zooplankton biomass from Lake Shaokatan, Minnesota, observed in 2013–2019. Total biomass; average biomass of calanoids, cyclopoids, large *Daphnia* spp., and small cladocerans; and the percent composition of large *Daphnia* spp. and small cladocerans sampled May–October are shown as yearly averages, with standard deviations in parentheses.

Year	Average biomass ($\mu\text{g/L}$)						% <i>Daphnia</i>	% small cladocerans
	Total biomass	Calanoids	Cyclopoids	Large <i>Daphnia</i>	Small cladocerans			
2013	1,110 (1,279)	106 (76)	48 (28)	913 (1,249)	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 3. Yellow Perch population dynamics from Lake Shaokatan, Minnesota, observed in July–August of 1996–2018. The total number of Yellow Perch individuals annually caught in gill nets is represented by N . Relative weight for Yellow Perch was calculated using intercept and slope values from Willis et al. (1991), and proportional size distribution (PSD) was calculated using stock and quality values in Willis et al. (1993). All values (excluding N and PSD) are shown as the annual mean, with standard deviations in parentheses. Mean length at age (LAA) was an average of observed lengths at specified ages.

Year	N	CPUE	Relative weight	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

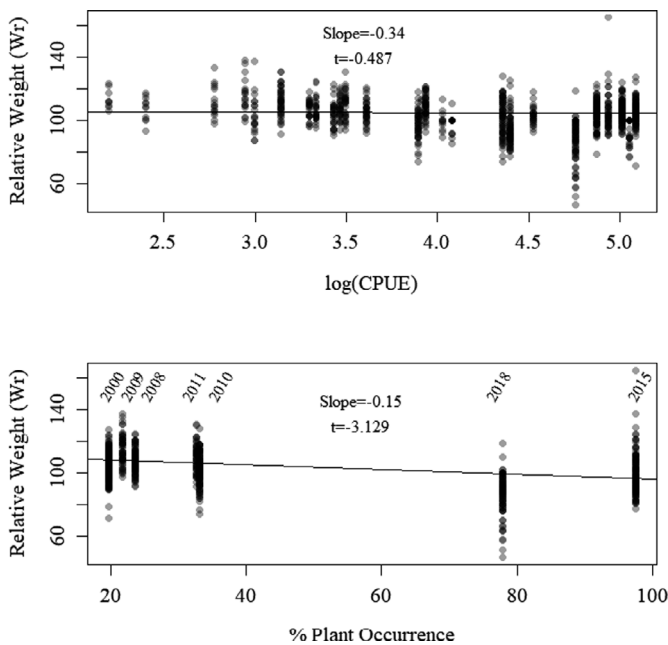


FIGURE 3. Yellow Perch relative weight (W_r) linear regression with log-transformed gill-net catch per unit effort (CPUE; top panel) and percent plant occurrence (bottom panel) collected in August in Lake Shaokatan, Minnesota, throughout 1996–2019. Random-coefficient mixed-effects models were used with $t \geq |2|$ being significant [i.e., $W_r \sim \text{Veg} + (1|\text{year})$]. As vegetation occurrence increases, the relative weight of individual fish decreases significantly. The CPUE did not show a significant relationship with relative weight.

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 the 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 1990s (MPCA 2009).

The qualitative observations of zooplankton community structure and greater biomass of large *Daphnia* spp. compared with 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 in 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, 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 supports 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. Yellow Perch caught in 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 relative weight was negatively correlated to vegetation occurrence in which the years containing higher occurrence of vegetation displayed a lower relative weight. A decrease in preferred zooplankton prey after the condition shift may also have further contributed 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 relative weight and total length 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 one Bluegill sampled) suggests that 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 gill nets (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 data set

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 with 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 relative weight 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 data sets 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 data set is key to understanding condition shifts as a whole.

ACKNOWLEDGMENTS

We thank the Sentinel Lakes Program and the agencies (MN DNR and MPCA) and personnel involved in field sampling and laboratory processing that contribute to the long-term monitoring of Lake Shaokatan. A special thanks is given to Dave Staples for statistical advice and the anonymous reviewers who aided in publishing this study. Funding for this project came from Bemidji State University and MN DNR (#176859). Financial assistance for presenting at conferences was also provided by a fall 2020 graduate student mini-grant from Bemidji State University. There is no conflict of interest declared in this article.

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