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Factors Affecting White Bass Abundance in Two Missouri River Reservoirs

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ABSTRACT Annual angler harvest of white bass (*Morone chrysops*) increased from 1985–2005 in Lake Oahe and Lake Sharpe, two mainstem Missouri River reservoirs in South Dakota. In 2006, harvest rates dropped appreciably in both reservoirs and remained low through 2015. It is hypothesized that a confirmed 2005 columnaris disease outbreak led to reduced annual angler harvest of white bass from both reservoirs. Mean annual angler harvest prior to the outbreak (1985–2005) in Lake Oahe decreased 65% and in Lake Sharpe decreased 57% post outbreak (2006–2015). To assess potential causes of sustained decreased adult white bass abundance in the reservoirs, we examined relationships among environmental (i.e., temperature, precipitation, water elevation, inflow) and biological factors (i.e., prey abundance, potential competitor abundance) with both age-0 and adult (>100 mm total length) white bass relative abundance before and after the columnaris disease outbreak. Prior to the outbreak, age-0 and adult white bass abundance was related to biological variables (i.e., age-0 fish abundance, adult walleye abundance and adult predator abundance) on Lake Oahe and Lake Sharpe. Following the outbreak, age-0 and adult white bass abundance was related to environmental variables (i.e., January gauge height, precipitation and temperature, April and July gauge height and precipitation) in both reservoirs. We hypothesize that since the columnaris disease outbreak reduced white bass abundance, environmental and biological factors have changed roles in affecting age-0 and adult white bass abundance (and angler harvest) in both reservoirs. Although these relationships are not necessarily causes of reduced abundance, we believe they can aid in management of white bass populations by allowing prioritization of biological and environmental factors related to age-0 and adult white bass abundance after columnaris disease-related die-offs.

KEY WORDS Angler, harvest, Lake Oahe, Lake Sharpe, white bass

White bass are popular among South Dakota anglers (Willis et al. 1997, 2002), particularly in the Missouri River impoundments. Estimated maximum yearly harvest of white bass was 57,499 in 2002 and 59,784 in 2005 on Lakes Oahe and Sharpe, respectively (Greiner et al. 2016). After 2005, annual angler harvest of white bass decreased to (and has remained) under 10,000 on Lake Oahe and under 21,000 on Lake Sharpe. In 2005, the white bass populations of Lakes Oahe and Sharpe both experienced confirmed (Wisconsin Veterinary Diagnostic Laboratories in Madison, Wisconsin) columnaris disease outbreaks resulting in high white bass mortality (Lott et al. 2005, Potter and Lott 2006). In Lake Oahe, mortality was estimated at 615,655 white bass, but unfortunately no estimate of the Lake Sharpe die-off was completed though anecdotal evidence suggests it was similar in magnitude to that experienced on Lake Oahe (Lott et al 2005). Since the columnaris outbreak in 2005, anglers from both Lakes Oahe and Sharpe have expressed concern regarding poor white bass fishing.

Periodic die-offs of white bass (columnaris disease-related or not) are common throughout the Midwest (Lott et al. 2005). Examples include, Lake Texoma, Oklahoma where thousands of white bass died in 2000 (Bean 2000), a major die-off was reported at Lake Shelbyville, Illinois in 2013 (Illinois Department of Natural Resources 2013), and hundreds of white bass died in Indian Lake, Ohio in 2014 (Wilson 2014). Iowa experienced a major white bass die-off in Big Creek Lake in 2012, and again in 2017 (Iowa Department of Natural Resources 2017). Recovery can be slow following a die-off. In 1998, Big Stone Lake in Minnesota had a white bass die-off, and it took 15 years for the population to recover (Weisman 2016). Although die-offs have been noted in popular press, specific causes are often summarized as "bacteria-related".

Columnaris is a disease caused by the bacterium *Flavobacterium columnare* (formerly known in the literature as *Cytophaga columnaris* and *Flexibacter columnaris*) and affects fish populations worldwide (Bullock et al. 1986, Bader and Starliper 2002, Mohammed and Arias 2015). The bacteria first adheres to the mouth, lips, cheeks, and gills, and then forms lesions or infects existing lesions before causing internal infection and mortality (Bullock et al. 1986, Rach et al. 2003). Virulence of the disease is dependent on the strain of bacteria involved (Decostere et al. 1998, 1999, Declerq et al. 2013). Characteristics of the disease are yellow or white spots or saddles on the body, head, or fins, as well as eroded fins (Decostere et al. 1998, Declerq et al. 2013). Transmission from fish to fish occurs through spores in the water (Wakabayashi 1993). *Flavobacteria* are present in most (if not all) freshwater aquatic, terrestrial and aquaculture environments (Durborow et al. 1998, Shrivastava and Berg 2015). The disease becomes lethal when environmental conditions (i.e., high water temperatures) are stressful for fish and preferable for columnaris disease (Wakabayashi 1991). Columnaris disease has been documented in numerous sport fish species, including largemouth bass (*Micropterus salmoides*), rainbow trout (*Oncorhynchus mykiss*), blue catfish (*Ictalurus furcatus*), striped bass and white bass (Macfarlane et al. 1986, Mourning et al. 1994, Steeger et al. 1994, Zeller and Cairns 2011, Fuller et al. 2014).

This ubiquitous bacterial disease is associated with high mortality in fish (Sahoo et al. 2010) and large-scale die-offs of fish populations due to columnaris have been noted (Scott and Bollinger 2014). For instance, channel catfish (*Ictalurus punctatus*) mortality can reach 80% in laboratory experiments (Figueiredo et al. 2005) and 100% in fish farms (Suomalainen et al. 2005) when infected with columnaris. At increased temperatures, 100% mortality due to columnaris disease infection has been noted in steelhead trout (Oncorhynchus *mykiss*) and coho salmon (O. kisutch; Holt et al. 1975). Due to its high lethality, columnaris causes economic losses by presenting challenges for aquaculture and sport fisheries (Sebastião et al. 2011, Farmer et al. 2013, Schrader et al. 2013). Annual losses resulting from columnaris in channel catfish farming alone are estimated at $30 million (Declerq et al. 2013).

Due to the noted prevalence of columnaris outbreaks throughout the Midwest and the documented ubiquity of the etiological agent, Flavobacterium *columnare*, it is likely that additional white bass die-offs will occur throughout the Midwest. Thus, it is important to identify and document factors that affect white bass populations before, during, and after these events. Since the columnaris outbreak in 2005 on Lakes Oahe and Sharpe, angler concerns regarding a prolonged decrease in white bass have occurred. We sought to determine if the 2005 die-off was responsible for the sustained decreased angler harvest, or if other factors could be contributing to reduced white bass harvest. We wanted to provide future management recommendations by (1) describing trends in white bass abundance before and after the die-off, 2) identifying conditions that may have led to the die-off, and 3) evaluating biological and environmental factors that are related with age-0 and adult white bass abundance in Lakes Oahe and Sharpe. A lack of available information regarding factors that influence age-0 and adult white bass abundance and, subsequently, annual angler harvest makes management of the species difficult.

STUDY AREA

Lakes Oahe and Sharpe form the fourth- and fifth-most upstream reservoirs of the Missouri River located in central South Dakota. Lake Oahe (150,000 ha) spans from Garrison Dam (RKM 2236.8) to Oahe Dam (RKM 1725.7), and has a maximum depth of 62 m. Lake Sharpe (23,020 ha) extends from Oahe Dam to Big Bend Dam (RKM 1589.1), and has a maximum depth of 24 m. Lake Oahe has numerous bays and three large tributaries, including the Grand, Moreau, and Cheyenne Rivers whereas Lake Sharpe has only two large bays and one large tributary, the Bad River. Recreational fisheries for walleye (*Sander vitreus*), northern pike (*Esox lucius*), smallmouth bass (Micropterus *dolomieu*), and white bass occur on both reservoirs.

METHODS

Fish sampling

We collected age-0 and adult (>100 mm total length) white bass during South Dakota Game, Fish and Parks' (SDGFP) annual fish population surveys on each reservoir from 1985 to 2015 on Lake Oahe and Lake Sharpe. On both reservoirs, we used standard experimental-mesh multifilament nylon gill nets (e.g., 10.7 m ×1.8 m deep with panels of the bar mesh sizes: 12.7 mm, 19.1 mm, 25.4 mm, 31.8 mm, 38.1 mm, 50.8 mm, and 63.5 mm) to collect adult white bass. Each year on Lake Oahe at nine locations, we set three standard gill nets overnight (approx. 20 h) on the bottom of a shallow depth zone (0–10 m) and three on the bottom of a deep depth zone (10–20 m), for a total of 54 gill nets (Potter et al. 2015; Fig. 1). Each year on Lake Sharpe, we placed three gill nets at four locations overnight in a shallow depth zone – (0–9 m) and three in a deep depth zone

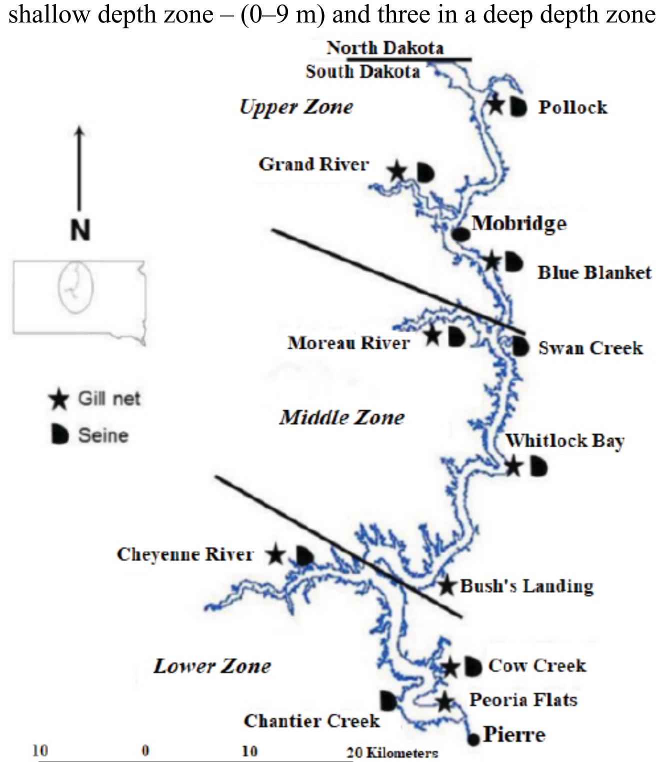

Figure 1. Gill net and seine sampling locations on Lake Oahe, South Dakota for white bass from 1985–2015. Figure adapted from Potter et al. 2015.

(> 9 m where possible; 24 total; Fig. 2; Greiner et al. 2016). We collected age-0 white bass from both reservoirs using 6.4 mm nylon mesh bag seines, measuring 30.5 m × 2.4 m with a 1.8 m × 1.8 m bag (Greiner et al. 2016). We used a

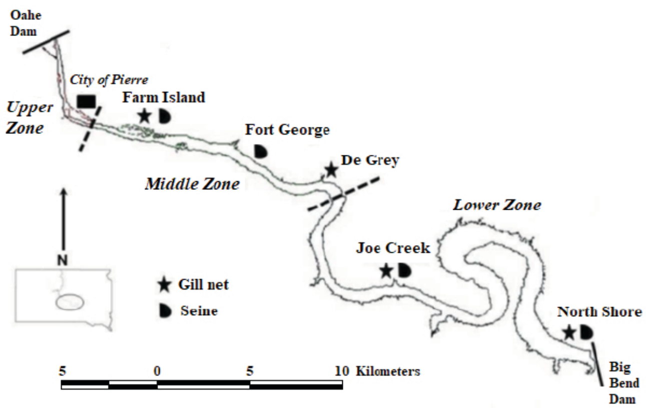

Figure 2. Gill net and seine sampling locations on Lake Sharpe, South Dakota for white bass from 1985–2015. Figure adapted from Greiner et al. (2016).

quarter-arc seine haul to collect age-0 fish following methods described in Martin et al. (1981). Each year, we made four seine hauls at nine sampling stations on Lake Oahe (36 total seine hauls) and four sampling stations on Lake Sharpe (16 total seine hauls). We designated adult white bass as stock length (≥150 mm TL) and quality length (≥ 230 mm total TL; Gabelhouse 1984). We measured fish abundance as catch per unit effort (CPUE) for seine (no./haul) and gill net (no./net night) catches and used this to monitor white bass age-0 and adult relative abundance. We averaged the number of age-0 white bass per seine haul by site and lake. Variability reflects variability between sites (not specific net catches). We used standard error (SE) as a measure of sample variability.

Angler catch rate and harvest

We collected Lake Oahe and Lake Sharpe angler catch data between 1986–2015. We determined white bass angler catch rate (no./angler/h) and harvest (no./year) from Lake Oahe using yearly open-water creel surveys (April–October) patterned after Schmidt (1975) and Soupir et al. (2006). Sampling included aerial counts of boat and shore anglers (n = 8 flights per month) to estimate fishing pressure. We conducted angler interviews at lake access areas (n = 1,000 to 2,000 per year) to estimate catch and harvest rates. We selected flight and interview dates using a stratified random design based on the assumption of different levels of fishing pressure for weekdays and weekend days/holidays. We assigned lake access areas for angler interviews using a stratified random design with probabilities of assignment differing by access area and month (Stone et al. 1994). We determined angler catch rate and harvest of white bass on Lake Sharpe using the same methods as those used on Lake Oahe until 2006. After 2006, we used angler interviews (n = 1,000 to 2,000 per year) in a modified bus route survey design (Jones and Robson 1991); bus route sampling locations are documented in Fincel et al. (2012). We randomly selected variables for the bus route sampling (i.e., day selection, shift time, route direction, starting location, route selection; Greiner et al. 2016). Since we were not comparing harvest between the two reservoirs, we assumed that different methods used to assess harvest on each reservoir did not affect our primary results.

Environmental variables

Precipitation (mean mm/month) and air temperature (mean °C/month) data were obtained from the NOAA (National Oceanic and Atmospheric Administration) climate website (NOAA 2018). South Dakota is divided into 9 divisions by NOAA, and the divisional values are weighted by area to compute statewide values (Karl and Koss 1984). We acquired peak flow, inflow, and gauge height data from the USGS (United States Geological Survey) water database website (USGS 2018). Gauges at Bismarck, ND, and Pierre, SD, were used for Lakes Oahe and Sharpe, respectively as they represent the nearest upstream USGS gauging locations. Seasonal environmental variables were selected for each month representing the four seasons including Spring (April), Summer (July), Fall (October), and Winter (January).

Statistical analysis —We used an unpaired t-test to test for differences between pre-die off (average for 1985-2005 grouped) and post-die off (average for 2006-2015 grouped) annual samples of age-0 white bass CPUE. Age-0 white bass CPUE prior to and after the outbreak did not meet normality assumptions, so were log10 transformed. All annual samples for adult white bass were grouped into pre-outbreak (1985-2005) and post-outbreak (2006-2015) for both Lakes Oahe and Sharpe and were log10 transformed if they did not meet normality assumptions (Shapiro-Wilk test; Shapiro and Wilk 1965). Due to non-normal data after log10 transformation, differences between pre-die off (before 2006) and post-die off (after 2006) adult white bass CPUE, associated length category (i.e., stock and quality length), and angler catch rates of white bass were assessed using a Kruskal-Wallis test (KW test; Blair and Hicks 2012, Amano et al. 2013). Statistical significance for all analyses was set at $\alpha = 0.10$. We performed all analyses in program R version 3.1.3 (R Development Core Team 2018).

Information Theoretic Approach

We used an information theoretic approach to assess which variables best supported trends in age-0 white bass abundance. Multiple linear models were used to examine the variation observed in age-0 and adult white bass abundance before and after the disease outbreak in both Lakes Oahe and Sharpe. Three main effects categories were hypothesized to be related to white bass relative abundance. These include characteristics of the 1) abundance of adult sport fish as potential predators for age-0 white bass and competitors for adult white bass, 2) abundance of prey fish as potential competitors for age-0 white bass and potential prey for adult white bass, and 3) seasonal abiotic variables that could influence production or capture of age-0 or adult white bass.

Seventeen single parameter candidate models were developed to encompass these three main categories (Table 1). We then combined logical parameters to create seven additional multi-parameter candidate models (Table 1) and used Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002) to determine which model best supported trends in white bass abundance. We evaluated models prior to the columnaris disease outbreak (1996–2005) and after the outbreak (2006–2015).

RESULTS

White bass abundance

Lake Oahe mean age-0 white bass CPUE was significantly higher following the columnaris outbreak (93.95 fish/haul; (T_{29} = -2.04; P = 0.05; 2006–2015) compared to before the columnaris outbreak (26.20 fish/haul; 1985–2005; Fig. 3). Age-0 CPUE remained stable from 1985–2013 and then

Table 1. Model names and terms for candidate models used to explain age-0 and adult white bass recruitment in Lakes Oahe and Sharpe from 1996 through 2015 (asterisks denote models used only for predicting age-0 white bass abundance).

Model Name	Model Definition
Adult_Pred	Adult sport fish abundance (excluding walleye and white bass)
Adult_WAE	Adult walleye abundance
Adult_WAE + Adult_Pred	Adult sport fish abundance (excluding walleye and white bass) + Adult walleye abundance
**Adult_WTB	Adult white bass abundance
Age-0_Fish	Age-0 fish abundance (excluding gizzard shad and white bass)
Age-0_Fish + Adult_WAE + Adult_Pred	Age-0 fish abundance (excluding gizzard shad and white bass) + Adult walleye abundance + Adult sport fish abundance (excluding walleye and white bass)
Age-0_GIS	Age-0 gizzard shad abundance
Age-0_Fish + Adult_WAE	Age-0 fish abundance (excluding gizzard shad and white bass) + Adult walleye abundance
Apr_GH	April gauge height
Apr_GH + Apr_P + Apr_T	April gauge height + April precipitation + April temperature
Apr_P	April precipitation
Apr_T	April temperature
Jan_GH	January gauge height
Jan_GH + Jan_P + Jan_T	January gauge height + January precipitation + January temperature
Jan_P	January precipitation
Jan_T	January temperature
Jul_GH	July gauge height
Jul_GH + Jul_P + Jul_T	July gauge height + July precipitation + July temperature
Jul_P	July precipitation
Jul_T	July temperature
Oct_GH	October gauge height
Oct_GH + Oct_P + Oct_T	October gauge height + October precipitation + October temperature
Oct_P	October precipitation
Oct_T	October temperature

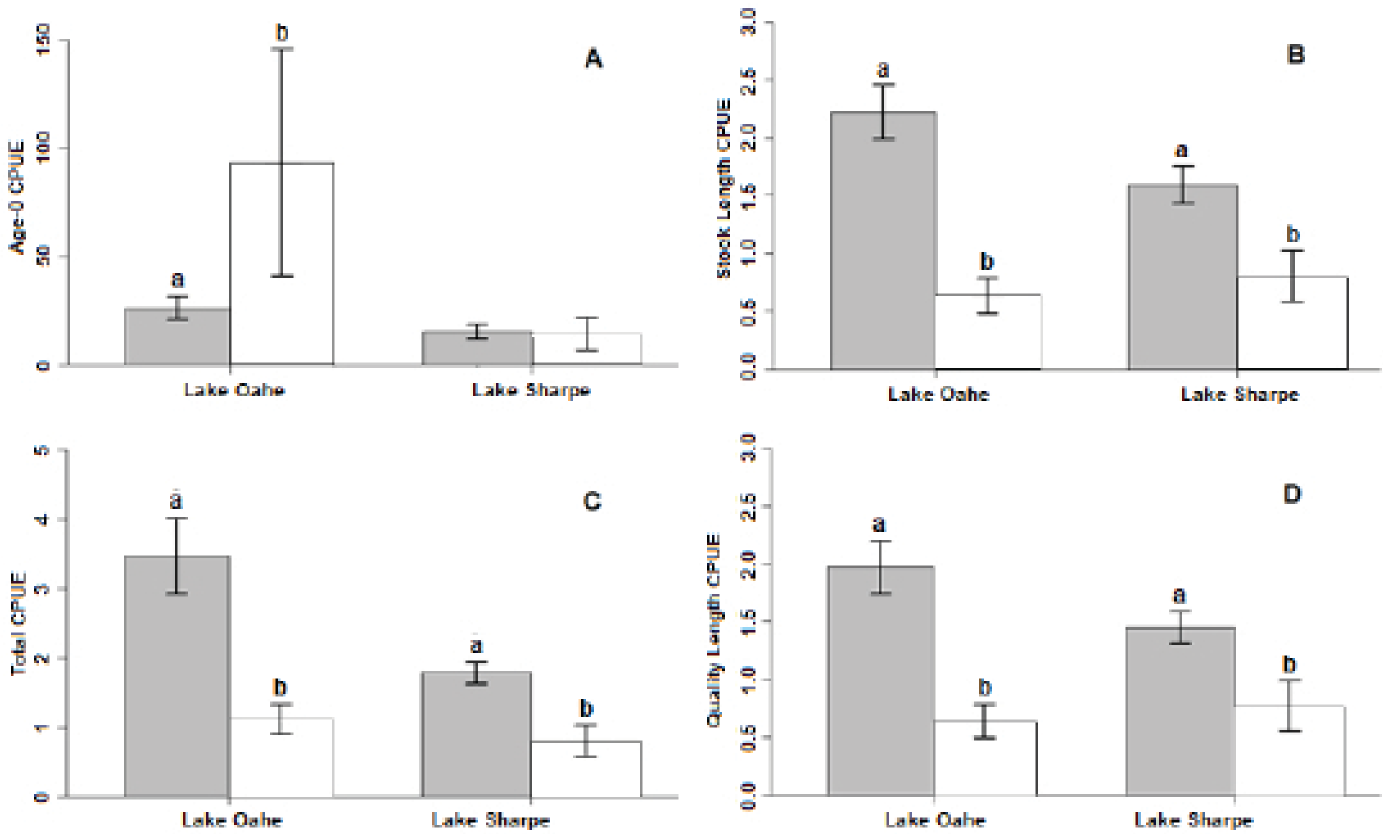

Figure 3. (A) Age-0 mean CPUE (Catch Per Unit Effort; from the prey fish survey), (B) ≥ stock-length CPUE, (C) total CPUE, and (D) ≥ quality-length CPUE (from the gillnet survey) for Lake Oahe and Lake Sharpe white bass from 1985–2015. Grey bars represent pre-outbreak (1985–2005) values, and white bars represent post-outbreak (2006–2015) values. Means with the same letter are not significantly different (Kruskal-Wallis test, $P \leq 0.10$). Error bars represent one standard error of the mean.

increased to 569.0 fish/haul in 2014; however in 2015, age-0 CPUE decreased to 12.50 fish/haul. Adult white bass CPUE ($\chi^2 = 4.59$; $P = 0.03$), stock-length CPUE ($\chi^2 = 12.91$; $P < 0.01$), and quality-length CPUE ($\chi^2 = 10.45$; $P < 0.01$) all decreased following the columnaris outbreak (Fig. 3). Mean adult CPUE was 7.28 fish/net (range 29.4 fish/net) prior to the outbreak and 1.41 fish/net (range 3.2 fish/net) after the outbreak.

Lake Sharpe age-0 CPUE (no./seine haul) remained similar before and after the columnaris outbreak ($T_{29} = 0.85$; $P = 0.39$; Fig. 3). Age-0 CPUE increased to 67.10 fish/haul in 1993 and peaked again at 74.80 fish/haul in 2008 (Fig. 4). Following 2009, age-0 CPUE remained under 23.30 fish/haul (Fig. 4). From 1986 to 1998, adult CPUE was erratic, peaking at 2.88 fish/net night in 1990. Mean age-0 CPUE was 12.07 fish/ haul (range 28.8 fish/haul) prior to the outbreak and 6.91 fish/haul (range 21.3 fish/haul) after the outbreak.

In Lake Sharpe, adult CPUE ($\chi^2 = 7.68$; $P < 0.01$), stock-length CPUE ($\chi^2 = 5.98$; $P = 0.02$), and quality-length CPUE ($\chi^2 = 6.08$; $P < 0.01$) were all significantly lower following the columnaris outbreak in 2005 (Fig. 3). Adult CPUE increased to 3.29 fish/net in 2003 and decreased to 0.04 fish/net in 2015 (Fig. 4). Mean adult CPUE was 2.86 fish/net (range 8.80 fish/net) prior to the outbreak and 0.83 fish/net (range 2.1 fish/net) after the outbreak.

White bass angler catch rate and harvest.— Lake Oahe angler catch rates prior to the columnaris outbreak (0.14 fish/angler/h) were higher than after (0.03 fish/angler/h; $\chi^2 = 3.96$; $P = 0.04$), as was angler harvest ($\chi^2 = 5.12$; $P = 0.02$; Figure 5). Lake Sharpe angler harvest of white bass prior to the columnaris disease outbreak was higher than after the outbreak ($\chi^2 = 3.57$; $P = 0.06$) though angler catch rates were similar between the two periods ($\chi^2 = 0.01$; $P = 0.93$).

Model selection

In general, models including biological variables best explained abundance of age-0 white bass in Lakes Oahe and Sharpe. In Lake Oahe, the biological factor model including age-0 fish abundance and adult walleye abundance was the most supported model ($w_i = 0.90$, log-likelihood = -39.66, 90% CI = -1.09–-0.55, r^2=0.78) for predicting age-0 white bass abundance prior to the outbreak of columnaris (Table 2). This model was ≥4.98 ΔAIC_c and weight of evidence

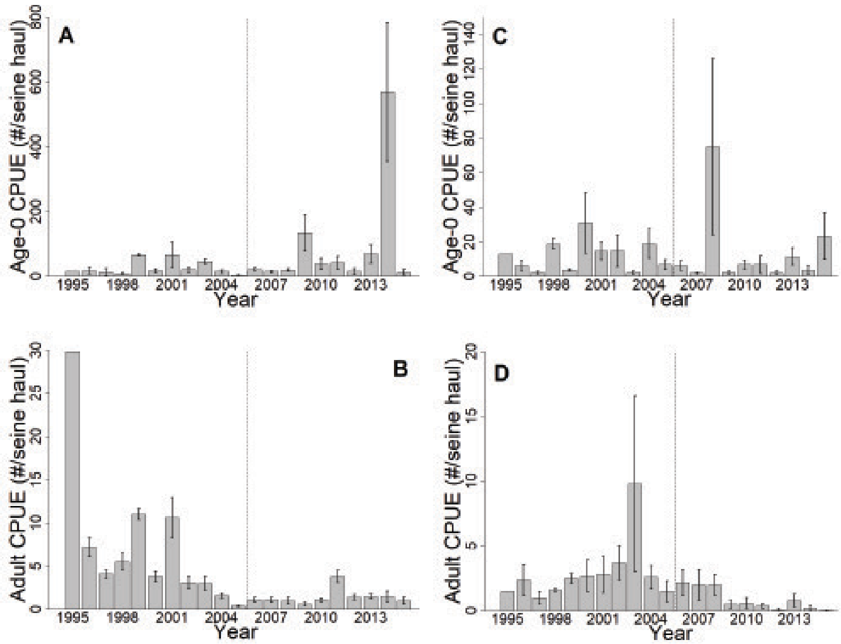

Figure 4. White bass CPUE (catch per unit effort) for A) Lake Oahe age-0 white bass, B) Lake Oahe adult white bass, C) Lake Sharpe age-0 white bass and D) Lake Sharpe adult white bass between 1995–2015 for Lake Oahe and Lake Sharpe. The dotted vertical line denotes the 2006 columnaris disease outbreak. Error bars represent one standard error.

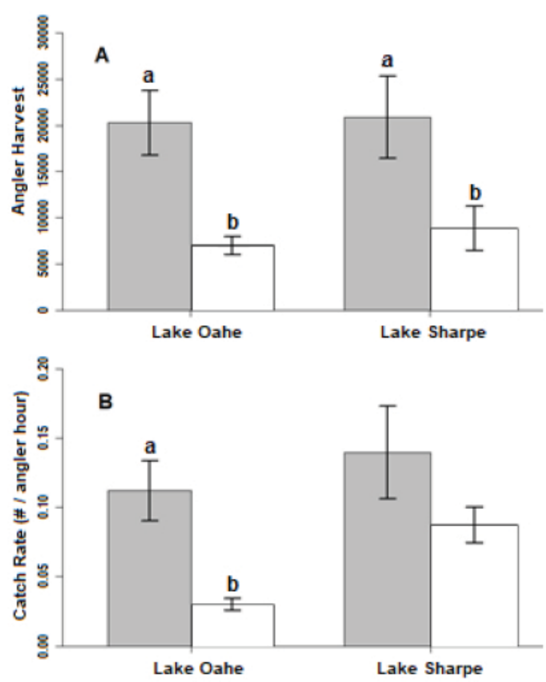

Figure 3. (A) Mean annual angler harvest (no./year) and (B) catch rate (no./angler hour) for Lake Oahe and Lake Sharpe white bass from 1985–2015. Grey bars represent pre-outbreak (1985–2005) values, and white bars represent post-outbreak (2006–2015) values. Means with the same letter are not significantly different (Kruskal-Wallis test, $P \leq 0.10$). Error bars represent one standard error of the mean.

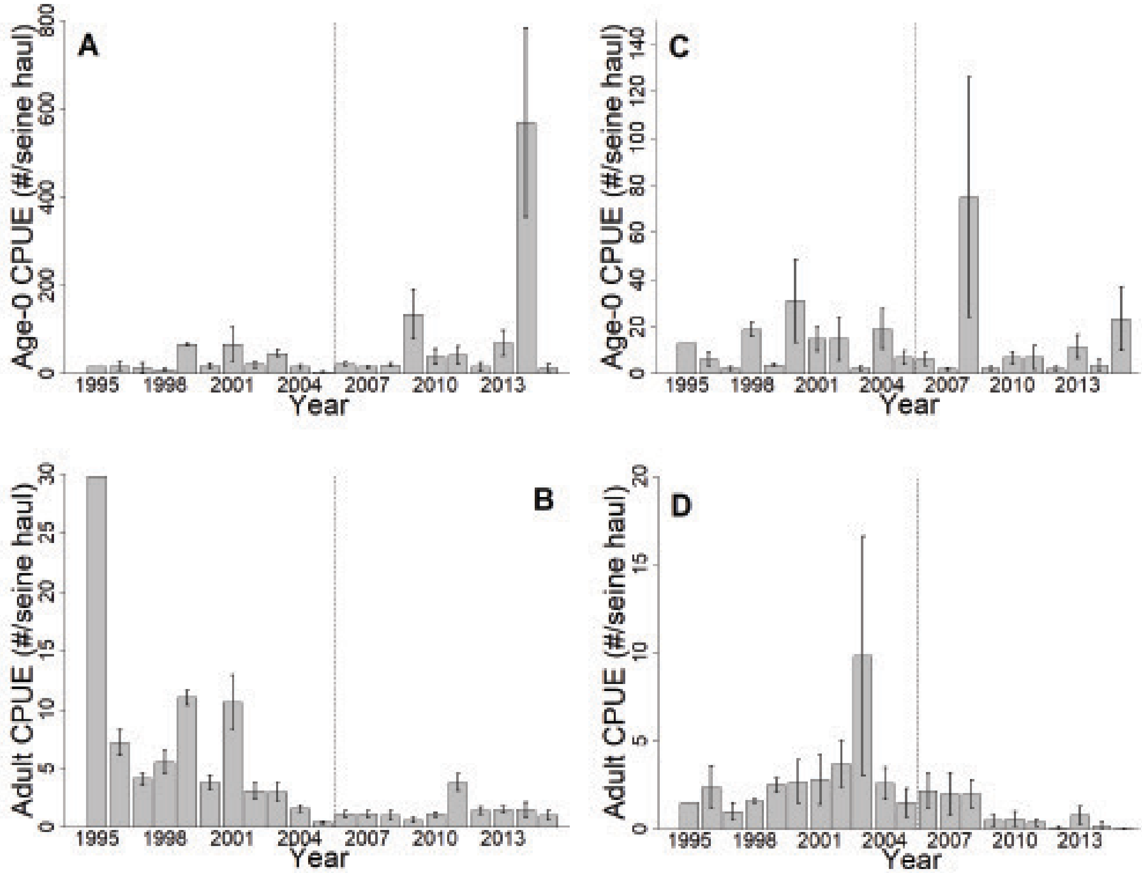

Figure 4. White bass CPUE (catch per unit effort) for A) Lake Oahe age-0 white bass, B) Lake Oahe adult white bass, C) Lake Sharpe age-0 white bass and D) Lake Sharpe adult white bass between 1995–2015 for Lake Oahe and Lake Sharpe. The dotted vertical line denotes the 2006 columnaris disease outbreak. Error bars represent one standard error.

supporting this model was 11.99 times greater than the next supported model. Additionally, age-0 fish abundance in combination with adult walleye abundance and adult predator abundance (w_i = 0.08, log-likelihood = -39.53, 90% CI = 0.03–0.06, r^2=0.77) and singularly (w_i = 0.02, log-likelihood = -45.43, 90% CI = 24.12–42.85, r^2=0.47) exhibited support. However, the January environmental model (w_i = 0.49, log-likelihood = -54.91, 90% CI = 47.84-285.57, r^2=0.82) best explained age-0 white bass abundance following the columnaris outbreak (Table 2). This model was ≥1.29 ΔAIC_c and weight of evidence supporting this model was 1.90 times greater than the next supported model. Moreover, environmental variables were included in three of the five top models for predicting age-0 white bass abundance following the outbreak in Lake Oahe.

In Lake Sharpe, age-0 fish abundance (w_i = 0.55, log-likelihood = -36.29, 90% CI = -3.36–1.40, r^2=0.38), January temperature (w_i = 0.15, log-likelihood = -37.61, 90% CI = -0.74–2.49, r^2=0.22) and January precipitation (w_i = 0.12, log-likelihood = -37.85, 90% CI = -24.65–18.90, r^2=0.19) best explained age-0 white bass abundance prior to the outbreak, although the October gauge height (w_i = 0.10, log-likelihood = -38.00, 90% CI = -3.41–3.71, r^2=0.17) and age-0 fish abundance coupled with adult walleye abundance (w_i = 0.09, log-likelihood = -36.16, 90% CI = -0.05–0.14, r^2=0.37) models also showed some support (Table 3). The age-0 fish abundance model was ≥2.64 ΔAIC_c and weight of evidence supporting this model was 3.74 times greater than the next supported model. After the columnaris outbreak on Lake Sharpe, April precipitation (w_i = 0.41, log-likelihood = -33.27, 90% CI = -8.42–2.86, r^2=0.25) showed the most support for predicting age-0 white bass abundance (Table 3). This model was ≥1.70 ΔAIC_c and weight of evidence supporting this model was 2.34 times greater than the next supported model. However, similar to Lake Oahe, models that included environmental variables (i.e., April gauge height (w_i = 0.16, log-likelihood = -34.18, 90% CI = -4.98–7.42, r^2=0.13)), July precipitation (w_i = 0.13, log-likelihood = -34.43, 90% CI = -1.59–4.89, , r^2=0.09) and October temperature (w_i = 0.12, log-likelihood = -34.46, 90% CI = -0.45–1.33, r^2=0.09) showed modest support for predicting age-0 white bass abundance on Lake Sharpe (Table 3).

In both Lakes Oahe and Sharpe, the most supported models for explaining adult abundance exhibited a notable

Table 2. Model selection results from 24 candidate models predicting age-0 white bass abundance in Lake Oahe, South Dakota, USA, from 1996 through 2015. Included are the top five models in the analyses with the number of estimated parameters (K), second order Akaike's Information Criterion (AIC_c), difference in AIC values relative to the best model (ΔAIC_c), and Akaike weights (w_i). Model parameter descriptions are included in Table 1.

Model	**K**	**AIC_c**	**ΔAIC**	w_i
Pre-Outbreak				
Age-0_Fish + Adult_WAE	4	90.755	0.000	0.899
Age-0_Fish + Adult_WAE + Adult_Pred	5	95.734	4.979	0.075
Age-0 Fish	3	98.364	7.609	0.020
Apr_P	3	102.063	11.308	0.003
Oct_P	3	102.283	11.528	0.003
Post-Outbreak				
Jan_GH+ Jan_P+ Jan_T	5	127.824	0.000	0.491
Age-0_Fish	3	129.110	1.286	0.258
Age-0_Fish + Adult_WAE	4	130.390	2.566	0.136
Jul_GH+ Jul_P+ Jul_T	5	131.209	3.385	0.090
Jan_GH	5	133.816	5.992	0.025

Table 3. Model selection results from 24 candidate models predicting age-0 white bass abundance in Lake Sharpe, South Dakota, USA, from 1996 through 2015. Included are the top five models in the analyses with the number of estimated parameters (K), second order Akaike's Information Criterion (AIC_c), difference in AIC values relative to the best model (ΔAIC_c), and Akaike weights (w_i). Model parameter descriptions are included in Table 1.

Model	**K**	**AIC_c**	**ΔAIC**	w_i
Pre-Outbreak				
Age-0_Fish	4	80.086	0.000	0.550
Jan_T	5	82.722	2.636	0.147
Jan_P	3	83.203	3.117	0.116
Oct_GH	3	83.495	3.409	0.100
Age-0_Fish + Adult_WAE	5	83.752	3.666	0.088
Post-Outbreak				
Apr_P	3	74.034	0.000	0.409
Adult_WAE	3	75.738	1.704	0.175
Apr_GH	3	75.863	1.829	0.164
Jul_P	3	76.360	2.326	0.128
Oct_T	3	76.421	2.387	0.124

change following the columnaris outbreak. Prior to the columnaris outbreak on Lake Oahe, age-0 fish abundance (w_i = 0.03, log-likelihood = -35.07, 90% CI = -4.46–11.87, r^2=0.41), adult walleye abundance (w_i = 0.06, log-likelihood = -34.28, 90% CI = -3.86–1.01, r^2=0.49) and other adult sport fish abundance (w_i = 0.08, log-likelihood = -34.10, 90% CI = -3.81–1.07, , r^2=0.50) were three variables found singularly or in combination with each other in all of the top five models (Table 4). The biological model including age-0 fish abundance coupled with adult walleye abundance and adult predator abundance (w_i = 0.50, log-likelihood = -27.65, 90% CI = -0.01–0.02, r^2=0.80) was the top model explaining adult white bass abundance prior to the outbreak. This model was ≥0.80 ΔAIC_c and weight of evidence supporting this model was 1.49 times greater than the next supported model. However, following the columnaris outbreak on Lake Oahe, July gauge height (w_i = 0.98, log-likelihood = -2.14, 90% CI = 0.07–0.19, r^2=0.86) was the most supported model, with all other models showing little support for predicting adult white bass abundance on Lake Oahe (Table 4). The July gauge height model was ≥9.68 ΔAIC_c and weight of evidence supporting this model was 122.88 times greater than the next supported model.

Prior to the columnaris outbreak on Lake Sharpe, January gauge height (w_i = 0.23, log-likelihood = -23.63, 90% CI = -2.68–1.62, r^2=0.18), July precipitation (w_i = 0.21, log-likelihood = -23.71, 90% CI = -3.95–2.41, r^2=0.17), April temperature (w_i = 0.20, log-likelihood = -23.74, 90% CI = -0.42–0.69, r^2=0.17) and adult predator abundance (w_i = 0.20, log-likelihood = -23.75, 90% CI = -0.51–0.49, r^2=0.17) were the most supported models for explaining adult white bass abundance (Table 5). All four of these models were similarly supported in explaining adult white bass abundance prior to the outbreak, only ≥0.24 ΔAIC_c apart. Additionally, July temperature (w_i = .16, log-likelihood = -23.99, 90% CI = -0.73–1.02, r^2=0.13) was found in the remaining most supported model. However, following the columnaris outbreak on Lake Sharpe, April gauge height (w_i = 0.50, log-likelihood = -9.31, 90% CI = -1.42–0.08, r^2=0.46), January gauge height (w_i = 0.34, log-likelihood = -9.70, 90% CI = -2.47–1.13, r^2=0.42) and October gauge height (w_i = 0.09, log-likelihood = -11.03, 90% CI = -0.46–0.20, r^2=0.27) were the most supported models to explain adult white bass relative abundance (Table 5) and four of the top five models included environmental variables. The April gauge height model was ≥0.78 ΔAIC_c and weight of evidence supporting this model was 1.47 times greater than the next supported model.

DISCUSSION

Prior to a white bass die-off, only models with biological factors (i.e., adult walleye abundance, adult sport fish abundance and age-0 fish abundance) showed strong support for explaining age-0 white bass CPUE on both reservoirs (as well as January temperature and precipitation and October gauge height on Lake Sharpe). Biotic factors (bluegill [*Lepomis macrochirus*] CPUE, black crappie [*Pomoxis nigromaculatus*] CPUE, age-0 walleye CPUE, and age 3+ white bass CPUE) have been found to have more importance than an abiotic factor in a candidate model set for explaining age-0 white bass CPUE (Deboer et al. 2013). Biological factors (e.g., predation) have been found to have an increased impact on striped bass abundance when such abundances are low (Buckel et al. 1999). However, with a smaller population size, environment factors are likely playing a larger role in dictating white bass abundance in our study systems. Quist et al. (2003) proposed a biotic-abiotic confining hypothesis to explain a similar relationship between age-0 walleye CPUE and 130- to 199-mm white crappie (*Pomoxis annularis*] CPUE in Kansas reservoirs. At low abundances, abiotic factors play a larger role in regulating age-0 white crappie CPUE, while biological factors have been found to play a larger role in regulating age-0 crappie CPUE at high abundances (Quist et al. 2003). It is possible that this is happening with age-0 white bass abundance in Lakes Oahe and Sharpe.

Despite high reproductive output, it appears these year classes have struggled to recruit to the fishery as suggested by the low adult CPUE in subsequent years. Previous research has found age-0 white bass CPUE to be positively related to precipitation and temperature (Pope et al. 1997), while others have found negative relationships between age-0 white bass abundance and these two variables (Beck et al. 1997). Temperature has been found to be positively related with hatch dates of white bass (Quist et al. 2002). Most of the columnaris disease-induced white bass mortalities in Lake Oahe during the 2005 die-off were observed in fish between 254–406 mm (Lott et al. 2005). It is possible that low levels of remaining columnaris disease infections (coupled with increased susceptibility of larger individuals to the outbreak, and/or smaller individuals to predation) is resulting in decreased adult white bass survival. However, no outbreaks have been identified since the 2006 outbreak.

Predation may also play a role in limiting the recovery of the Lake Oahe and Lake Sharpe white bass populations. White bass are a common diet item for walleye (Fincel et al. 2014) and smallmouth bass (Fincel et al. 2019) in both reservoirs. Additionally, smallmouth bass abundance has increased in both Lake Oahe and Lake Sharpe over the 1995-2015 period and could be influencing recruitment of abundant age-0 white bass (Fincel et al. 2015). Together, these two apex predators could be limiting white bass recruitment in Lake Oahe and Lake Sharpe. Regardless of the cause, drastically reduced angler catch rates and harvest remain on Lake Oahe and Lake Sharpe over a decade following the die-off.

Post die-off, primarily models with environmental factors (i.e., January and July gauge height, precipitation and temperature for Lake Oahe, April precipitation and gauge height, July precipitation and October temperature for Lake

Table 4. Model selection results from 24 candidate models predicting adult white bass abundance in Lake Oahe, South Dakota, USA, from 1996 through 2015. Included are the top five models in the analyses with the number of estimated parameters (K), second order Akaike's Information Criterion (AIC_c), difference in AIC values relative to the best model (ΔAIC_c), and Akaike weights (w_i). Model parameter descriptions are included in Table 1.

Model	**K**	**AIC_c**	**ΔAIC_c**	w_i
Pre-Outbreak				
Age-0_Fish + Adult_WAE + Adult_Pred	5	71.965	0.000	0.497
Age-0_Fish + Adult_WAE	4	72.763	0.798	0.333
Adult_Pred	3	75.703	3.738	0.077
Adult_WAE	3	76.064	4.099	0.064
Age-0_Fish	3	77.645	5.680	0.029
Post-Outbreak				
Jul_GH	3	11.991	0.000	0.983
Jul_GH + Jul_P + Jul_T	5	21.671	9.680	0.008
Jan_P	3	22.684	10.693	0.005
Adult_WAE	3	23.231	11.240	0.004
Adult_WAE + Adult_Pred	4	25.289	13.298	0.001

Table 5. Model selection results from 24 candidate models predicting adult white bass abundance in Lake Sharpe, South Dakota, USA, from 1996 through 2005. Included are the top five models in the analyses with the number of estimated parameters (K), second order Akaike's Information Criterion (AIC_c), difference in AIC values relative to the best model (ΔAIC_c), and Akaike weights (w_i). Model parameter descriptions are included in Table 1.

Model	**K**	**AIC_c**	**ΔAIC_c**	w_i
Pre-Outbreak				
Jan_GH	3	54.763	0.000	0.227
Jul_P	3	54.917	0.154	0.210
Apr_T	3	54.981	0.218	0.203
Adult_Pred	3	54.999	3.409	0.202
Jul_T	3	55.478	0.715	0.159
Post-Outbreak				
Apr_GH	3	26.124	0.000	0.504
Jan_GH	3	26.899	0.775	0.342
Oct_GH	3	29.557	3.433	0.091
Jul_P	3	31.572	5.448	0.033
Age-0_Fish	3	31.735	5.611	0.031

Sharpe) showed strong support for explaining age-0 white bass CPUE on both reservoirs. High flushing rates, low discharge and warmer June/July air temperatures on Lake Oahe, and cooler January/April/May air temperatures, low discharge and lower inflow on Lake Sharpe have been found to be positively related to age-0 white bass abundance (Beck et al. 1997). Age-0 white bass abundance has been found to be positively correlated with mean daily April/June air temperature and precipitation in small South Dakota lakes (Pope et al. 1997). It could be that we found models with April precipitation (but not April temperature) to be strongly supported in explaining age-0 white bass abundance because of system-size dependent factors.

Before the die-off, only biological factors (i.e., age-0 sport fish abundance, adult walleye abundance, and adult predator abundance) singularly or in combination showed strong support for explaining adult white bass abundance on Lake Oahe. On Lake Sharpe, only a single biological variable showed strong support for explaining adult abundance (adult predator abundance). Prior research has found both age-0 and adult white bass abundance decreased due to predation on early life stages in the presence of another adult predator, white perch (*Morone americana*; Madenjian et al. 2000). It seems that post die-off, adult predator abundance is still affecting age-0 and adult white bass abundance, but not to the extent as environmental factors such as July gauge height, precipitation and temperature and January precipitation on Lake Oahe.

Post die-off, primarily models with environmental factors (i.e., January precipitation and July gauge height, precipitation and temperature for Lake Oahe, April precipitation and gauge height, July precipitation and October temperature for Lake Sharpe) showed strong support for explaining adult white bass CPUE on both reservoirs. The single biological factor model decreased in weight post-outbreak compared to prior to the outbreak. April inflow has been found to be positively related to year-class strength of age-1 white bass in Virginia reservoirs (DiCenzo and Duval 2002). Inflow increases with increased precipitation and gauge height, so it is reasonable that we found models with April precipitation and gauge height to be strongly supported in explaining adult white bass abundance.

Mitigation of factors negatively related with age-0 and adult white bass abundance should be considered now that environmental factors have a stronger influence post outbreak than prior outbreak. A previous study on the four mainstem Missouri River reservoirs in South Dakota found positive relationships between April inflow and white bass abundance, contrary to our findings (Beck et al. 1997). Spring inflow was positively related with age-0 white bass CPUE in 3 of 16 Kansas reservoirs studied between 1981-2000 (Schultz et al. 2002). Quist et al. (2002) found a positive relationship between mean inflow and frequency of white bass hatch dates on Glen Elder Reservoir, KS. We found April precipitation to be related to age-0 white bass abundance, similarly to prior research (Pope et al. 1997). Although precipitation cannot be modified, inflow can likely be modified to maximize age-0 white bass abundance

Management implications of our findings are relevant in the Midwest and in any water that has white bass die-offs. Aquatic resource professionals can use data on conditions conducive to a die-off to liberalize harvest regulations for an at-risk species, maximizing the fishing opportunities prior to a die-off. Although all freshwater fish species are probably susceptible to columnaris disease (Wakabayashi 1991), fisheries can be managed to ensure that fishing opportunities exist in the event of a die-off. For instance, if Lake Oahe's white bass fishery collapsed, other sport fisheries could be exploited to mitigate the economic impact of decreased fishing opportunities on the reservoir. Management should shift to maximizing fisheries for non-affected species after a die-off, because recovery of an affected species after a die-off can take decades. Also, treated feeds and chemical baths may be feasible methods for reducing the lethality and recovery time following a die-off in small water bodies and in aquaculture operations. However, in large reservoirs, further research is necessary to develop feasible methods for mitigating the impacts of columnaris disease on white bass angler harvest.

Our research illustrates potential management opportunities when annual angler harvest has been decreased after a white bass die-off. Managers need to thoroughly document conditions and factors when die-offs occur to increase understanding. Simply documenting die-offs alone will provide insight into patterns, allowing managers to forecast the frequency with which die-offs of white bass may occur in their management areas. In addition, managers need to attempt to mitigate the impact of die-offs, so that strategies regarding the mitigation of impacts of die-offs can be developed. Research also needs to be directed into what factors affect age-0 recruitment to catchable adult sizes post-outbreak. Although we examined relationships with age-0 and adult abundances of white bass, we did not directly investigate the mechanisms with which factors affect such abundances.

MANAGEMENT IMPLICATIONS

We found that a columnaris outbreak did not negatively affect age-0 white bass abundance in Lake Oahe or Lake Sharpe, but did negatively affect adult white bass abundance and angler harvest on both reservoirs. Columnaris outbreaks could negatively affect age-0 white bass recruitment to adulthood. Further, we found that the relative role environmental and biological factors play was potentially altered by a columnaris outbreak. It seems that at reduced abundance, environmental factors play a greater role than biological factors in dictating both age-0 and adult white bass abundance.

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