Effects of harvest, natural mortality, and escapement on reservoir Walleye populations

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Abstract

Walleye *Sander vitreus* are commonly introduced to reservoirs and provide valued fisheries. Walleye populations are lost though harvest and natural mortality in all systems, but escapement may also reduce reservoir populations. However, the effects of harvest, natural mortality, and escapement loss on reservoir Walleye populations are not known. Our objective was to quantify Walleye harvest, natural mortality, and escapement in two Iowa reservoirs to understand how these factors limit populations. We also assessed Walleye behaviors and compared them among escaped, harvested, and in-lake Walleye to determine if behavior was associated with fate. Walleye were radio tagged beginning in October 2016 and tracked through May 2019. Telemetry was used to estimate annual core and home ranges, seasonal depth use, and movement rates. Detection histories were analyzed using a multi-state capture-recapture model with environmental covariates to estimate weekly harvest, natural mortality, and escapement. Harvest was greater in Big Creek than Brushy Creek and was higher in April through July compared to other months. Natural mortality was positively related to water temperature but did not differ between systems. No Walleye escaped from Big Creek (fish barrier on spillway) but escapement at Brushy Creek (no fish barrier) was positively related to mean water levels during April. During 2017-2018, annual Walleye escapement ranged from 22-47% at Brushy Creek (0% at Big Creek), harvest ranged from 13-27%, and natural mortality ranged from 36-38%. Walleye depth was shallower during spring and summer when escapement occurred, intermediate in fall, and deepest during winter. Escaped Walleye at Brushy Creek used greater depths and moved less than in-lake Walleye; however, other behaviors did not differ among Walleye groups. Our results suggest escapement can have a larger effect than harvest on reservoir Walleye populations in systems without physical barriers and should be taken into consideration when managing reservoir Walleye fisheries.

Walleye *Sander vitreus* provide highly valued recreational fisheries in North America (Kerr 2011) with over 3 million anglers and almost 44 million days spent angling for Walleye in 2011 (U.S. Department of the Interior et al. 2011). Due to its popularity among anglers, Walleye is one of the most commonly stocked species in U.S. reservoirs (Eby et al. 2006). Walleye fisheries are often harvest oriented and fish loss via harvest can be significant for Midwestern reservoirs, resulting in
reduced Walleye abundance (Baccante and Colby 1996; Quist et al. 2010). Walleye catch and harvest
often varies seasonally, with higher rates during the spring and early summer than during summer,
fall, and winter (Stone and Lott 2002; Quist et al. 2010). Conversely, warmer temperatures during
summer can lead to decreased feeding, poor condition, and reduced growth (Hokanson 1977) that may
increase natural mortality rates (Quist et al. 2002, 2004). However, little data is available regarding
Walleye natural mortality rates, particularly on the southern edge of their range where thermal stress
is greater and natural mortality rates may be higher compared to northern latitudes (MacLean and
Magnuson 1977; Quist et al. 2002, 2003). Although stocking efforts can bolster populations without
self-sustaining natural reproduction, stocked Walleye often have low survival rates (Olson et al. 2000;
Jennings et al. 2005; Weber et al. 2020; Weber and Weber 2020), making it difficult to establish and
maintain reservoir Walleye populations. Therefore, understanding the relative sources of reservoir
Walleye loss is critical for sustainable management of recreational Walleye fisheries.

Beyond mortality, an important but often overlooked factor that may threaten the
sustainability of reservoir sport fish populations is escapement over spillways and through outlet
structures (Louder 1958; Lewis et al. 1968; Paller et al. 2006; Weber et al. 2013; Weber and
Flammang 2019) that complicates the maintenance of populations (Louder 1958; Wahl 1999). For
instance, approximately 10,000 fishes (nine different species) escaped from an Illinois, USA 65–ha
lake during a 23–month period (Louder et al. 1958). Likewise, 31% of a Largemouth Bass
Micropterus salmoides population in a new impoundment escaped within a year (Lewis et al. 1968).
Escapement of Walleye may also be problematic, with annual estimates of escapement from a large
reservoir in Iowa, USA approaching 26%, with the economic loss of escaped Walleye near $400,000
(Weber et al. 2013; Weber and Flammang 2019). Although a few studies have quantified Walleye
escapement from reservoirs, these took place on large systems with water control structures that
operate differently and have contrasting water releases relative to smaller spillway reservoirs. Aside
from potential variation due to differing water control structures, escapement may be influenced by
several environmental factors. Escapement can vary among seasons, with greater escapement
occurring in spring during periods of higher water levels and discharge rates (Lewis et al. 1968;
Powell and Spencer 1979; Wolter et al. 2013). For example, Weber and Flammang (2019) found
Walleye escapement from a bottom-draw water control reservoir was positively related to mean April
discharge, suggesting most escapement occurs during spring spawning periods. Water levels may also affect Walleye escapement rates from spillway reservoirs, but the timing, magnitude, and relationship with water levels may be different than those described in reservoirs with control structures. Thus, a better understanding of Walleye escapement from spillway reservoirs is critical for improved management of these systems.

Walleye display unique seasonal behavior and movement patterns that may affect their vulnerability to escapement or harvest. Walleye is a migratory species and can have expansive home ranges (Palmer et al. 2005; Bellgraph et al. 2008) due to nomadic behavior (Ager 1977; Williams 1997). During spring, Walleye spawn in shallow water over rocky substrate (Eschmeyer 1950; Johnson 1961; Priegel 1970; Kerr et al. 1997; Raabe and Bozek 2012) that may attract them to reservoir dams and spillways (Martin et al. 2012). These reservoir Walleye behaviors could affect fish harvest or escapement, as mobile fish may be more likely to encounter anglers (Palmer et al. 2011; Parsons et al. 2011; Monk and Arlinghaus 2017; Sylvia et al. 2020) or spillway areas. However, the potential effects of how reservoir Walleye behaviors affect harvest or escapement are unknown.

We conducted radio telemetry of adult Walleye in two central Iowa spillway reservoirs over two and a half years to gain a better understand the relative effects of harvest, natural mortality, and escapement for populations in these unique systems. First, telemetry encounter data were combined with a suite of environmental covariates in a multi-state capture-recapture model to estimate harvest, natural mortality, and escapement probabilities. Second, tracking data were used to determine Walleye depth use, movement rates, and annual core and home range sizes. Third, we compared behavior metrics among Walleye that were harvested, survived, and escaped to determine if behaviors varied among groups. This combination of analyses allowed us to assess how different mechanisms are influential in limiting reservoir Walleye populations as well as evaluate how behavior may affect Walleye harvest, natural mortality, and escapement. We hypothesized Walleye harvest, escapement, and movement rates would be greater during spring, Walleye would use shallower water during spring due to spawning behavior, and escapement would be positively related to spring water level. During summer, we predicted escapement, harvest, and movement rates would decline, fish would use greater depths, and natural mortality would increase due to thermal stress. Of the three potential sources of fish loss, we hypothesized harvest would play the biggest role in regulating Walleye
populations. Finally, we predicted escaped and harvested Walleye would have greater movement rates and larger ranges than in-lake Walleye due to a greater probability of fish encountering anglers and spillway areas. Results of this study will provide new insights into factors resulting in the loss of reservoir Walleye that can be used to improve management of reservoir Walleye populations.

**Methods**

**Study Area**

Big Creek Lake is a 357-ha reservoir located in Polk County, Iowa, USA (Figure 1). Filled in 1972, the reservoir has a large watershed (~20,000 ha), much of which is used for agriculture. In the mid-1990s, Big Creek underwent extensive maintenance, including installation of armored shorelines to prevent shoreline erosion and dikes to control incoming sediment. Due to concerns regarding emigration of sportfishes from Big Creek (B. Dodd, Iowa Department of Natural Resources (DNR), personnel communication), a physical barrier was installed at the spillway in 2012. The barrier consists of eight chain–link top rails (4.06 cm outer diameter) stacked in a horizontal fashion with 5.08 cm openings between rails (73.7 cm tall). The rails are made of 16–gauge galvanized steel and are attached to vertical spillway posts with line rail clamps. Big Creek has a mean depth of 5.9 m, a maximum depth of 16.3 m, and is largely void of emergent coarse woody habitat (hereafter CWH). However, more than 45 brush piles were installed by the Iowa DNR from 2007-2010 as fish habitat. Aquatic vegetation present in Big Creek includes American Pondweed *Potamogeton nodosus*, Coontail *Ceratophyllum demersum*, and Sago Pondweed *Potamogeton pectinatus*, in addition to non–native Curly–leaf Pondweed *Potamogeton crispus*. The prey base for piscivores in Big Creek consists mainly of Gizzard Shad *Dorosoma cepedianum* that were present in the system beginning in the 1980s. A large winterkill in 2000-2001 was thought to have eradicated the population and none were found during standardized fish sampling from 2001–2013; however, low numbers were detected in 2014 before increasing substantially during summer 2015 (A. Otting, Iowa DNR, unpublished data).

Brushy Creek Lake is a 280-ha reservoir located in Webster County, Iowa, USA, (Figure 1) that was completed in 1998. Approximately 65 km north of Big Creek, Brushy Creek has a similarly sized watershed (~21,000 ha) that is also used primarily for agriculture. The reservoir has a mean depth of 8.8 m, a maximum depth of 22.9 m, and contains a large amount of coarse woody habitat as...
well as aquatic vegetation. Aquatic vegetation in Brushy Creek includes American Pondweed, Coontail, Duckweed *Lemma minor*, Sago Pondweed, Southern Naiad *Najas guadalupensis*, Watermeal *Wolffia* spp., Two-leaf Watermilfoil *Myriophyllum heterophyllum*, and Water Stargrass *Heteranthera dubia*. Additionally, the system contains two non-native species of vegetation, Brittle Naiad *Najas minor* and Curly-leaf Pondweed. Gizzard Shad are present in the spillway basin but not the reservoir; alternatively, Bluegill *Lepomis macrochirus*, Black Crappie *Pomoxis nigromaculatus*, and Yellow Perch *Perca flavescens* are the primary prey base for piscivorous species. Thermoclines develop at approximately 6 m in both systems during the summer months.

**Transmitter Implantation**

Adult Walleye \[n=42\text{/lake; mean TL = 516 mm (range 381-703 mm)\]} were collected at each lake via boat electrofishing and short-term gill net sets and implanted with radio transmitters (ATS, Isanti, Minnesota; F1835, 14 g in water, 1,003 d battery life, 0.3%-2.8% body weight). Before implantation, surgical equipment was soaked in 4% chlorhexidine (disinfectant) and rinsed with distilled water (Burger et al. 1994; Harms 2005). Walleye were measured (TL, mm) and weighed (g) before being placed ventral side up into a wooden V-shaped tray with four mounted electrodes and immobilized using electroanesthesia (Maxtens 1000 TENS Unit) via pulsed direct current (Vandergoot et al. 2011). After being placed on the wooden tray, fish were immobilized by slowly increasing electrical intensity, after which iodine ointment was applied along the linea alba. During surgeries, fresh water was continuously passed over the gills. A scalpel was used to make an incision anterior to the pelvic girdle (Schramm and Black 1984; Clapp et al. 1990) that was enlarged using scissors until transmitters could be admitted into the body cavity (Hart and Summerfelt 1975). After transmitter insertion, a 16-gauge hypodermic needle was used to create an exit hole for the whip antenna anterior to the anus. Incisions were closed using size 2/0 Maxon sutures (Medtronic, Inc.; Dublin, Ireland) with an interrupted cruciate suture and an additional single interrupted suture if necessary. After the incision was closed, iodine ointment was applied and fish were returned to a tank of recirculating water to recover. Walleye were monitored for approximately 20 minutes post-implantation until they resumed normal swimming behavior, after which they were released near the
surgery location. Initial tagging efforts occurred during fall 2016 (19 Walleye), with additional tags being deployed during spring and fall throughout the study (n=64 during remaining periods).

Radio Telemetry

Tracking of telemetered Walleye began in late October 2016 and ended in late May 2019, approximately 950 days from the first tagging event. After tags were deployed, tracking was conducted on a weekly basis at each lake during the open water season (March-November) and bi-weekly during safe ice conditions (typically January-February). Range testing prior to tracking events indicated radio tags could be detected to a depth of 9 m in each lake. Additionally, downstream spillway locations at each lake were scanned for escaped Walleye on a regular basis during and after flow events. An ATS model R4000 receiver connected to a 3-element folding Yagi radio antenna was set to maximum volume and gain and the lake perimeter was slowly scanned until a fish was detected. Detected fish were approached and the gain was turned down until the tag signal was barely noticeable and signal strength was equal in all directions, at which point fish location and lake water depth (m) at each fish location were recorded (Guy et al. 1994). When three or more consecutive tracking events indicated no movement for a tagged Walleye, it was considered dead and tracking data were reviewed to determine when the last live location occurred (Wagner and Wahl 2011).

Capture-Recapture Analysis

Radio telemetry of fish can have imperfect detection (Melnychuk 2012) and not every Walleye could be located during each tracking event. Therefore, individual Walleye live encounter histories were generated from telemetry data and analyzed in Program MARK (White and Burnham 1999) using a live capture multi-state model to generate maximum-likelihood estimates of detection probability ($p$), true survival ($S$; hereafter survival), and transition ($\Psi$) probabilities (White et al. 2006). The multi-state model is an extension of the Cormack-Jolly-Seber (CJS) live recapture model that incorporates multiple areas, permitting simultaneous inference and separation of survival and location estimates. Multi-state models assume tagged individuals are representative of the population, number of individuals tagged is known, tagging does not affect survival, recaptures and releases are made within brief time periods relative to the time between tagging, recaptures do not affect later survival or recapture, fates of tagged individuals among and within cohorts are independent, and individuals in a cohort have the same survival and recapture probability for each time interval.
Unequal tracking intervals (i.e., tracking did not occur exactly every 7 d) were adjusted in Program MARK when initializing the model to provide standardized weekly estimates of survival, detection, harvest, and escapement throughout the entire study.

Our model consisted of three possible states where Walleye could be detected: live within their respective lakes (L; Big Creek and Brushy Creek), harvested and reported by an angler (H), or escaped to their respective tailraces (E; Figure 2). Transition probabilities from lake to harvested ($\Psi_{L-H}$; harvest probability) and lake to escaped ($\Psi_{L-E}$; escapement probability) were estimated while other possible state transitions (escaped to lake, harvested to lake, and escaped or lake) were illogical and were fixed to zero. For example, a Walleye encounter history of “LLH” over a three-occasion sampling period would be modelled as

$$P(\text{LLH}) = \phi_{L1}^L p_{L2}^L \phi_{L2}^H p_{H3}^H$$

where $\phi_{r,s}^i$ represents the combined probability that a Walleye alive in state $r$ at time $i$ is alive and in state $s$ at time $i+1$; thus,

$$\phi_{r,s}^i = S_r^i \Psi_{r,s}^i$$

where $S_r^i$ is the probability of surviving from time $i$ to $i+1$, given an animal is in state $r$ at time $i$, and $\Psi_{r,s}^i$ is the probability that an animal in state $r$ at time $i$ is in state $s$ at time $i+1$ given it survives to time $i+1$. When an individual goes missing and is detected on a later occasion (i.e., an encounter history of “L0H”), the uncertain state of the fish at occasion 2 leads to two probability paths:

$$\phi_{L1}^L (1 - p_{L2}^L) \phi_{L2}^H p_{H3}^H$$

where the Walleye survived and stayed in the lake (L) but was not seen in the lake on occasion 2, was harvested (L-H) and reported as harvested on occasion 3, or

$$\phi_{L1}^H (1 - p_{L2}^H) \phi_{L2}^{HH} p_{H3}^H$$

where the Walleye was harvested (H) and not reported on occasion 2, but was reported as harvested on occasion 3. Therefore, the expected frequency of Walleye with an encounter history of “L0H” is:

$$R_L^1[\phi_{L1}^L (1 - p_{L2}^L) \phi_{L2}^H p_{H3}^H + \phi_{L1}^{HH} (1 - p_{L2}^H) \phi_{L2}^{HH} p_{H3}^H]$$

where $R_L^1$ represents the number of Walleye tagged and released in the lake on occasion 1 (Cooch and White 2019).

Although it was possible for fish to be harvested and reported after escaping ($\Psi_{E-H}$), Walleye were assigned a final state of “E” after escaping and harvest from the spillway basin was not
estimated due to a low number of fish with this fate that would have not estimated in the multi-state model. Radio-tagged Walleye were also implanted with PIT (passive integrated transponder) tags, PIT antenna arrays were present on both spillways, spillways were regularly checked for radio tags, and no Walleye that escaped went undetected; thus, detection probability of escaped Walleye at both lakes was fixed to one. Because of perfect detection and tagged Walleye escapement from Brushy Creek only occurring in April, escapement was fixed to zero in all other months. Similarly, because no radio-tagged Walleye escaped from Big Creek during the study, Walleye escapement probability at Big Creek was fixed to zero. Angler tag reporting rate at Big Creek Lake was estimated as 0.75 from 2010 to 2012 (Dodd and Otting 2012); therefore, detection probability of Walleye in the harvested state (i.e., reporting rate) was fixed to 0.75 in both lakes. As other studies have found Walleye reporting rates that were considerably lower than 0.75 (Quist et al. 2010; Vandergoot et al. 2012), we also assessed the potential effects of lower reporting rates (0.50, 0.25) on harvest estimates. Because the change in reporting rate had a minimal effect on harvest estimates (e.g., change in weekly harvest probability <0.001), we continued the modeling process with a fixed reporting rate of 0.75. When a tagged Walleye was physically captured in the Brushy Creek spillway during opportunistic sampling events, it was returned to the lake and entered in the dataset as a new individual (n=1), allowing for the continued use of this individual in the dataset without biasing survival, detection, escapement, or harvest estimates (Weber et al. 2013). Finally, one Walleye at Big Creek and six Walleye in Brushy Creek were never encountered following tagging and were not included in the capture-recapture analysis.

We developed a priori hypotheses to assess potential factors influencing Walleye weekly survival, detection, and transition probabilities among states. Our model set evaluated the effect of lake (Big or Brushy), month, year, water temperature, as well as a number of water level metrics (mean, minimum, maximum, coefficient of variation) on a weekly basis. Comparing all possible combinations of effects on survival, detection, and transition parameters was unrealistic; therefore, we used a hierarchical modeling approach (Doherty et al. 2012) and ran a set of models where model complexity within survival (variation among lakes and time), lake to harvest transition (variation among lakes and time), and lake to escaped transition (variation through time at Brushy) was retained while the effects of lake, month, and water temperature on detection probability were evaluated. After
evaluating different structures for detection, the structure with the most support was retained while
evaluating combinations for survival. Similarly, when the best supported structure for survival was
determined, the effects of lake, month, water temperature, and water level metrics on transition
probabilities for escapement and harvest were assessed. We also grouped months when evaluating
model structures for harvest, as other studies have shown distinct monthly trends in Walleye harvest
(Quist et al. 2010; Dodd and Otting 2012). Additionally, grouping months allowed us to reduce the
number of model parameters, increasing precision of harvest estimates. Hypotheses were modelled
and compared in Program MARK using Akaike’s Information Criterion corrected for small sample
size ($\text{AIC}_c$; Burnham and Anderson 2002), as a reliable goodness-of-fit statistic does not exist for
multi-state models (Conn et al. 2004). Akaike weights ($W_i$) were calculated to address uncertainty
regarding top model selection (Burnham and Anderson 2002). Beta ($\beta$) estimates in the results are
presented on a logit-transformed scale. As our primary objective was comparing the relative effects of
different sources of fish loss, survival estimates were converted to natural mortality (natural mortality
$= 1 – \text{true survival}$) to facilitate comparisons against harvest and escapement.

Home Range, Depth Use, and Movement

Kernel density estimation (KDE) methods were used to estimate annual Walleye core ranges
(50% contour) and home ranges (90% contour; Powell 2000). This method uses animal locations to
calculate a density function and determine a minimum area that includes a fixed percentage of the
density distribution (Fuller et al. 2005). Fish locations were plotted in ArcGIS and individual Walleye
ranges were estimated using the ‘kernelUD’ function in package ‘adehabitatHR’ (Calenge 2006). The
default method of this function is the bivariate normal kernel function using a reference bandwidth for
the smoothing parameter $h$ of $h = \sigma n^{(-1/6)}$, where $n$ is the number of fish locations and $\sigma = 0.5 (\sigma_x + \sigma_y)$,
where $\sigma_x$ and $\sigma_y$ are the standard deviations of the x and y coordinates of locations for an individual
Walleye, respectively (Calenge 2006). Annual core and home ranges were only estimated for Walleye
with a minimum of 15 locations within a given year during the study. Potential differences in Walleye
ranges were tested with analysis of variance (ANOVA) using the ‘lme’ function in package ‘nlme’
(Pinheiro et al. 2018) with a fixed effect of lake and year included as a random effect.
Minimum weekly movement rates (m/week, hereafter movement rates) and depth at Walleye locations (hereafter depth) were calculated for each individual Walleye and averaged within seasons, defined as spring (March-May), summer (June-August), fall (September-November), and winter (December-February). Movement rates were calculated as the minimum in-water distance between two consecutive locations divided by weeks between locations. Movement rates were only calculated for Walleye with consecutive locations occurring within two weeks to prevent biasing movement rates for fish located infrequently. Movement rates were not calculated for Walleye during the winter due to intermittent tracking as well as limited fish locations during this period. Depth represented the lake depth at Walleye locations, which could represent the depth of the fish if they were located on the bottom or the lake depth that they were suspended above if they were not located on the bottom. Both Walleye depth and movement rates were log-transformed to normalize the residuals. Analysis of variance (ANOVA) was used to test for differences in depth and movement rates; season, lake, and their interaction were included as fixed effects with year as a random effect. Post-hoc analyses were conducted using the ‘emmeans’ package (Lenth 2019) to compare estimated marginal means adjusted for multiple comparisons using the Tukey method.

After calculating behavior metrics, mean values for individual Walleye were pooled within each lake based on fish fates and compared using Welch’s t-tests to determine whether depth, movement rate, core range size, and home range size differed among harvested, in-lake, and escaped Walleye. Walleye with final fates of alive, dead, and missing were all included in the in-lake Walleye group, as we did not want to exclude data for these individuals that was collected while they were alive and in the lake. All statistical analyses were conducted using Program R version 3.5.2 (R Core Team 2018) and were considered significant at $\alpha = 0.05$.

Results

Radio Telemetry

A total of 83 adult Walleye were radio tagged from fall 2016 to spring 2019, resulting in a total of 1,106 individual locations (706 in Big Creek, 400 in Brushy Creek) with an average of 13 locations (SD = 12.4) per individual. Of the 83 tagged Walleye, 12 were never relocated with the radio telemetry receiver after being released: one in Big Creek and 11 in Brushy Creek. However, of the 11
Brushy Creek Walleye that were never relocated after release, three were detected in the spillway after escaping, one of which was later harvested from the spillway, and two were harvested in lake and reported by anglers. A total of 9 of 41 (22%) radio-tagged Walleye escaped from Brushy Creek during the study; one Walleye that escaped in 2017 was recaptured in the spillway and returned to the reservoir, after which it escaped a second time in 2018. Therefore, there were a total of 10 Walleye escapement events during the study: three in 2017, four in 2018, and three in 2019, with all Walleye escaping between April 10 and 22. Additionally, there were 15 confirmed Walleye natural mortalities (nine in Big Creek, six in Brushy Creek) and 19 harvested Walleye (10 in Big Creek, nine in Brushy Creek). Of the nine Walleye harvested and reported at Brushy Creek, three were harvested from the tailrace pool after escaping from the reservoir (33% of escaped Walleye). At both lakes, the majority (14 of 19 fish; 74%) of harvest occurred from May through July in 2017 and 2018.

**Capture-Recapture**

The best supported model structure for detection probabilities indicated Walleye detection varied between lakes and with water temperature (Table 1). Detection probabilities were greater in Big Creek than Brushy Creek (β = 1.357; 95% CI = 1.149 to 1.566) and increased with water temperature (β = 0.028; 95% CI = 0.021 to 0.036). In both lakes, detection probabilities were lowest in March 2019 and greatest in July 2018, ranging from 0.50 to 0.80 in Big Creek and 0.20 to 0.51 in Brushy Creek (Figure 3). No other models comparing detection probability were supported (ΔAICc > 29; Table 1).

The most supported structure for natural mortality included the effect of water temperature, with natural mortality increasing with increasing water temperature (β = -0.036; 95% CI = -0.065 to -0.007). Weekly natural mortality estimates ranged from 0.003 to 0.021 in both lakes, with the lowest and highest estimates occurring at water temperatures of 1.1°C and 29.5°C, respectively (Figure 4). There was some support for the effect of lake on natural mortality (ΔAICc = 1.36) but the effect of lake did not differ from zero (β = -0.705; 95% CI = -1.598 to 0.189). No other model structures used to estimate natural mortality received support (ΔAICc > 2.72; Table 1).

After determining the best structure for detection and natural mortality, models were developed to compare factors associated with Walleye transition to harvest; three had ΔAICc < 1.0 and W_i > 0.15 whereas all other candidate models had less support (ΔAICc > 1.98, W_i < 0.10; Table 1).
Our top model indicated Walleye harvest varied between lakes and months, with greater harvest from April through July compared to the rest of the year ($\beta = 2.042; 95\% \text{ CI} = 0.550$ to $3.533$). The point estimate of harvest probability was also greater in Big Creek than Brushy Creek ($\beta = 0.791$) but this difference was not significant, as the confidence interval did not differ from zero ($95\% \text{ CI} = -0.278$ to $1.861$). Weekly Walleye harvest probability was $0.015$ ($95\% \text{ CI} = 0.010$ to $0.021$) at Big Creek from April through July and $0.002$ ($95\% \text{ CI} = 0.0005$ to $0.0070$) during the rest of the year. Estimates at Brushy Creek were similar, with April-July weekly harvest probability estimated at $0.007$ ($95\% \text{ CI} = 0.003$ to $0.014$) and at $0.0009$ ($95\% \text{ CI} = 0.0002$ to $0.0040$) during other months (Figure 5). There was some support for models without a lake effect ($\Delta AIC_c = 0.42$) where harvest was estimated at $0.010$ ($95\% \text{ CI} = 0.008$ to $0.013$) during April-July and at $0.002$ ($95\% \text{ CI} = 0.0004$ to $0.0060$) during other months. There was also some support for greater harvest during May and June ($\Delta AIC_c = 0.67$) where harvest was estimated at $0.023$ ($95\% \text{ CI} = 0.014$ to $0.039$) during May-June and at $0.004$ ($95\% \text{ CI} = 0.002$ to $0.008$) during other months.

Finally, the top model indicated weekly escapement probabilities at Brushy Creek during April were best described by mean weekly water level. Although the effects of other water level metrics on escapement during April were also assessed, the second ranked candidate model (weekly minimum water level during the month of April; $\Delta AIC_c = 0.55, W_i = 0.33$) received less support and produced similar parameter estimates ($0.018$ to $0.217$) with greater standard errors, while the third ranked model received little support ($\Delta AIC_c = 2.53; \text{ Table 1}$). Weekly mean water level during April was positively related to Walleye escapement probability ($\beta = 9.304; 95\% \text{ CI} = 1.991$ to $16.617$), with weekly estimates ranging from $0.034$ to $0.289$ at water levels from $0.05$ m to $0.28$ m (Figure 6).

Weekly harvest, natural mortality, and escapement probabilities from our top model were each applied as the sole source of fish loss (i.e., escapement, harvest, and natural mortality acting independently instead of cumulatively) to a theoretical population of 10,000 Walleye > $381$ mm (minimum tagging size in this study) to evaluate how temporal variation in weekly estimates of harvest, natural mortality, and escapement contribute to fish loss on from October 2016 through October 2018. In Big Creek, annual harvest was estimated at $27.1\%$ ($95\% \text{ CI} = 2.6\%$ to $31.5\%$) while natural mortality was estimated at $38.9\%$ ($95\% \text{ CI} = 23.6\%$ to $59.8\%$) from October 2016 to October 2017 and $38.1\%$ ($95\% \text{ CI} = 22.6\%$ to $59.7\%$) from October 2017 to October 2018. Estimates of
harvest from Brushy Creek were lower, resulting in an annual harvest estimate of 13.3% (95% CI =
1.0% to 18.3%) with natural mortality ranging from 37.8% (95% CI = 22.8% to 58.8%) from October
2016 to October 2017 to 37.0% (95% CI = 21.9% to 58.5%) from October 2017 to October 2018.
While mortality estimates were similar between lakes and years, escapement estimates at Brushy
Creek were more variable, ranging from 21.9% (95% CI = 15.1% to 31.7%) during April 2017 up to
46.5% (95% CI = 31.7% to 67.8%) during April 2018 (Figure 7).

Home Range, Depth Use, and Movement

Annual core and home ranges were estimated for 35 Walleye with at least 15 locations during
a given year: 13 in Big Creek in 2017, 11 in Big Creek in 2018, three in Brushy Creek in 2017, and
eight in Brushy Creek in 2018. Walleye core ranges ($F_{1,33} = 12.58, P = 0.001$) and home ranges ($F_{1,33}
= 22.28, P < 0.001$) both differed between lakes. Walleye in Big Creek had large core ranges (mean =
107.1 ha, SE = 13.6 ha) and home ranges (mean = 237.0 ha, SE = 13.1 ha) relative to core (mean =
40.0 ha, SE = 16.5 ha) and home ranges (mean = 126.9 ha, SE = 25.3 ha) in Brushy Creek. Walleye
average core and home ranges encompassed 33% and 72% of the surface area of Big Creek,
respectively, while encompassing 14% and 46% of the surface area of Brushy Creek.

Water depth at Walleye locations varied among seasons ($F_{3,987} = 8.84, P < 0.0001$) and
between lakes ($F_{1,987} = 54.08, P < 0.0001$) but not the interaction ($F_{3,987} = 1.84, P = 0.14$). Depth was
greater in Brushy Creek (mean = 4.35 m, SE = 0.45) than Big Creek (mean = 3.03 m, SE = 0.26).
Across seasons, depth was greatest during winter (mean = 5.55 m, SE = 0.82) followed by fall (mean
= 3.47 m, SE = 0.31), spring (mean = 3.09 m, SE = 0.28), and summer (mean = 2.91 m, SE = 0.26;
Figure 8). Movement rates also differed between lakes ($F_{1,129} = 9.60, P = 0.002$) with lower
movement in Brushy Creek than Big Creek (Figure 8). However, no differences in Walleye
movement rates were detected among seasons ($F_{2,129} = 2.80, P = 0.06$) or the lake-season interaction
($F_{2,129} = 1.71, P = 0.18$)

Walleye that escaped from Brushy Creek (n = 6) were located in deeper water (4.83 m [SD =
0.90]) than those that remained in-lake (n = 20; 3.76 m [SD = 0.92]; Welch's $t$-tests: $t_{(8)} = -2.55, P =
0.03$; Figure 9). Walleye harvested from Brushy Creek (n = 4) were found at similar depths (4.45 m
[SD = 1.81]) as those that escaped ($t_{(4)} = 0.39, P = 0.72$) and remained in-lake ($t_{(3)} = -0.74, P = 0.51$).
Movement rates in Brushy Creek were lower for Walleye that escaped (n = 4; 239.73 m/week [SD =
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compared to those that remained in-lake (n = 17; 548.3 m/week [SD = 361.91]; \( t_{(11)} = 2.56, P = 0.03 \)) while movement for harvested Walleye (n = 3; 505.75 m [SD = 490.91]) did not differ from either escaped (\( t_{(2)} = -0.90, P = 0.46 \)) or in-lake Walleye (\( t_{(2)} = 0.14, P = 0.90 \)). No significant differences in core and home ranges were detected between harvested and in-lake Walleye in Big Creek (50% core range: \( t_{(9)} = -0.41, P = 0.69 \); 90% home range: \( t_{(10)} = -0.74, P = 0.48 \)) or escaped and in-lake Walleye in Brushy Creek (50% core range: \( t_{(4)} = 0.02, P = 0.98 \); 90% home range: \( t_{(3)} = 0.17, P = 0.87 \); Figure 9). Harvested Walleye had insufficient locations for home range estimation.

**Discussion**

Understanding factors related to and the magnitude of Walleye escapement from reservoirs is critical for successful management of these dynamic systems. Additionally, determining the relative effects of fish loss via escapement compared to harvest and natural mortality is critical, as escapement can lead to major reductions in population densities, further complicating management. Our capture-recapture analysis revealed escapement can be a significant source of fish loss in spillway reservoirs without barriers and may result in greater loss than harvest or natural mortality, particularly during years with high water levels during spring. Harvest is commonly cited as an important factor regulating Walleye populations (Sullivan 2003; Quist et al. 2004, 2010) and fisheries management often focuses on regulating harvest as a means of managing populations because it is more easily estimated and managed through alterations in creel and size limits (Sullivan 2003; Isermann 2007) compared to natural mortality.

While harvest can alter populations, our results indicate natural mortality has a larger effect than harvest on the loss of Walleye from these populations. We estimated Walleye annual exploitation at 13% for Brushy Creek and 27% for Big Creek, with harvest seven times higher from April through July compared to the rest of the year. Similarly, in a highly exploited reservoir in Kansas, USA (2000-2002 annual Walleye exploitation estimate = 68%), 85% of Walleye exploitation occurred from April to June, with 54% of tag returns occurring during May (Quist et al. 2010). Baccante and Colby (1996) summarized Walleye exploitation for 46 populations with a median exploitation rate of 21% and only four populations with a mean over 30%. Big Creek Lake is located adjacent to the largest metropolitan area in Iowa (Des Moines metropolitan area <24 km, approximately 700,000 people).
and receives considerable fishing pressure (Dodd and Otting 2012). Although Big Creek exploitation estimates are above average, estimates up to 68% have been reported for other Midwest reservoirs (Quist et al. 2010) and up to 94% in Canadarago Lake, New York, USA (Willms and Green 2007). Spatiotemporal variation in harvest mortality further illustrates the importance of understanding the effects of anglers and other sources of fish loss on Walleye populations, as a thorough understanding and quantification of fish loss is imperative when devising management plans.

Our model estimates indicated natural mortality is a greater contributor to fish loss than harvest or escapement during some years. Variation in weekly Walleye natural mortality estimates in each lake were best explained by water temperature, with natural mortality positively associated with water temperatures and estimates ranging from 36-38% annually. Due to the harvest-oriented nature of many Walleye fisheries, natural mortality estimates are not widely available (Bozek et al. 2011). However, our estimates are comparable to those from an unexploited reservoir in Pennsylvania that ranged from 32-41% (Kocovsky and Carline 2001a). Other studies in Midwestern reservoirs estimated total annual mortality of Walleye ranged from 5-46% in an Iowa reservoir (Weber and Flammang 2019) to 40-60% in eight Kansas reservoirs (Quist et al. 2004). Walleye prefer water temperatures ranging from 21-23°C, with an optimum temperature of 22°C and an upper lethal limit near 31°C (Hokanson 1977; Hasnain et al. 2010). During our study, temperatures ranged from 1-29°C, with mean weekly surface temperatures typically exceeding the thermal optimum from early June to early October. Kocovsky and Carline (2001b) found decreased Walleye condition and feeding activity during summer in Pymatuning Reservoir, Pennsylvania when average temperatures were generally greater than 22°C and proposed the thermal regime played a significant role in structuring the Walleye population. Similarities in latitude and size between Pymatuning Reservoir and our study systems suggest thermal conditions are important in regulating reservoir Walleye populations in Iowa as well.

In addition to harvest and natural mortality, Walleye escapement from reservoirs, although rarely assessed, can have a major effect on populations. In this study, escapement had similar or larger effects on the loss of Walleye from the population compared to natural mortality and harvest. Walleye escapement was only observed in Brushy Creek during April and increased with weekly mean water level. Weber et al. (2013) hypothesized Walleye escapement would be greater during spring in a large...
reservoir with a bottom-draw water control structure (Lake Rathbun, Iowa) due to spawning activity, but the hypothesis received little support; instead, mean daily discharge throughout the year had the greatest influence on escapement probability. The discrepancy between Rathbun Lake and results observed here may be due differences in water level regulation structures; Brushy Creek has a spillway overflow outlet while releases from Rathbun Lake occur via a bottom-draw system. We observed Walleye using shallow water during spring and summer that could have resulted in increased escapement over spillway systems, while bottom-draw control structures are in deeper water. Walleye have an affinity for demersal habitats (Kerr et al. 1997) that could lead to year-round escapement through bottom-draw reservoirs compared to small impoundments with spillways, particularly with exponential increases in flow rates. In our study, weekly estimates of escapement probability ranged from 0.03 with a mean spillway water level of 0.05 m to 0.29 with a spillway level of 0.28 m. Escapement was relatively consistent at water levels up to 0.1 m, after which escapement probability substantially increased. Other studies have found a similar relationship between escapement and discharge (Navarro and McCauley 1993; Weber et al. 2013; Weber and Flammang 2019; Meerbeek and Weber 2020), supporting the idea of a discharge threshold that, when passed, leads to dramatic increases in escapement. Armbruster (1962) found that nearly 20,000 Walleye escaped from Berlin Reservoir, Ohio, USA during a five-year period, with nearly half of Walleye being mortally wounded during emigration and the majority of escapement occurring during rapid lake level reductions. Weber et al. (2013) also found Walleye daily escapement from Rathbun Lake, Iowa increased exponentially as mean daily discharge increased from 8 to 61 m$^3$/s. Similarly, escapement from Rathbun Lake was consistently low during years with fewer than 200 days of discharge greater than 14 m$^3$/s but increased exponentially to 26% when 235 days had discharge greater than 14 m$^3$/s (Weber and Flammang 2019). The positive relationship between discharge and escapement is particularly concerning, as large precipitation events in the Midwest are predicted to increase in intensity in the future (Melillo et al. 2014). Increased precipitation will lead to increased discharge from reservoirs that could have adverse effects on Walleye population. Weber and Flammang (2019) found similar rates of escapement (2-26%) and mortality (6-46%) for Walleye over 10 years at Rathbun Lake, Iowa and suggested the combination of these mechanisms could lead to depleted populations and decreased angling opportunities.
Walleye used shallower water during summer in both systems, intermediate depths during spring and fall, and deeper water during the winter. As Big Creek and Brushy Creek are spillway reservoirs, escapement probability likely increases as Walleye move from deep winter habitats to shallower water in spring. Walleye select areas with coarse substrates during spawning (Martin et al. 2012) and most coarse substrate in our study systems is on or near the dam, which likely contributes to escapement during this period. While we did detect some differences in Walleye behavior between escaped fish and those that remained in-lake (escaped Walleye used deeper water and moved less), those differences were contrary to our hypotheses, potentially due to small sample size in each group. Thus, there was little support indicating that individual fish behaviors contributed to their fate.

Walleye had greater movement rates and larger ranges in Big Creek than Brushy Creek, likely due to environmental differences (water clarity, vegetation, coarse woody habitat, prey fish assemblages, etc.) between reservoirs. Larger movements by Walleye in Big Creek due to turbidity and active foraging may lead to greater harvest by increasing their chances of encountering anglers. Walleye may also be more susceptible to harvest during spring, as use of shallower depths during this time can increase vulnerability to angling, particularly by shore anglers. Additionally, spring water temperatures are closer to the thermal optima, while feeding activity is reduced at the extremes of their thermal range (Kitchell et al. 1977).

Reservoir fish escapement can lead to the creation of productive tailrace fisheries, with the emigration of recreationally valued fish acting as a stocking program for these systems (Jacobs and Swink 1983; Trammell et al. 1993; Schultz et al. 2003). However, reservoir fish communities consist largely of stocked non-native piscivores (Rahel 2000; Eby et al. 2006) which, after escaping, can threaten the integrity of downstream ecosystems through competition, hybridization, and predation (Martinez et al. 1994; Spoelstra et al. 2008). Additionally, downstream systems may not provide suitable conditions to sustain stocked piscivores during extreme thermal events and periods of low discharge, potentially resulting in high mortality rates of escaped fishes. Thus, reducing escapement is of interest to many fisheries managers, which might be accomplished by manipulating discharge rates or implementing fish barriers. A variety of barrier types exist (e.g., acoustic, bubble, electric, light, physical) that could be applied depending on spillway design. Physical barriers are easy to implement, relatively inexpensive, and can be effective in reducing escapement over reservoir spillways.
However, non-physical barriers are more feasible for bottom-draw outlet structures and may reduce escapement (Flammang et al. 2014; Weber et al. 2016) although implementation of these methods is not as simple. No escapement of tagged Walleye was observed at Big Creek, suggesting the physical barrier currently in place on that system is effective at preventing escapement of adult Walleye. However, the two systems also differ in terms of morphometries, with the spillway at Brushy Creek being located directly on the dam while the spillway at Big Creek is partially isolated from the main lake via a canal (Figure 1). Therefore, Walleye movement from the main basin at Big Creek through the canal to the spillway area may be restricted, inherently leading to lower escapement probabilities.

Although radio tags typically have high detection rates, detection becomes more difficult at greater depths and higher conductivity. Because of the availability of deep water in both lakes, depth data may have been biased shallow relative to actual depths used by Walleye. Similarly, limited detections of individual Walleye in both lakes may have led to biased home range estimates (Seaman et al. 1999). Although our home range estimates may not be directly comparable to other studies with greater numbers of individual fish locations and higher detection rates, our primary objective was to compare behavior between Walleye groups in our study, and we found little evidence to support any behavioral differences between fish that escaped and those remaining in-lake. However, we had a relatively small sample size for each group that may have limited our ability to distinguish differences in behavior between Walleye groups. Despite the same number of Walleye being tagged at each system, fewer total Walleye locations were recorded at Brushy Creek, likely due to greater depth and habitat complexity compared to Big Creek. While using raw counts of Walleye with known fates of harvest, natural mortality, and escapement would be biased due to imperfect detection, we used a capture-recapture model with Walleye encounter histories to estimate these parameters while accounting for imperfect detection probabilities, resulting in accurate harvest, natural mortality, and escapement estimates (White and Burnham 1999). Therefore, estimates presented here provide accurate information regarding harvest, natural mortality, and escapement rates of Walleye in small impoundments.

Cumulatively, our results provide a greater understanding of how harvest, natural mortality, and escapement regulate spillway reservoir Walleye populations as well as offers insight into how behavior relates to the different sources of fish loss. We found most Walleye harvest occurs during
spring and summer, natural mortality is greatest when water temperatures are high, and escapement only occurs in April and is positively related to water level. In both systems, Walleye used moderate depths and exhibited the greatest movement during spring that could lead to increased escapement in systems with spillways. Although escaped Walleye at Brushy Creek used greater depths and moved less than in-lake fish, behavior was otherwise similar among Walleye groups, suggesting individual behavior has little effect on these sources of fish loss. While 22% of Walleye escaped from Brushy Creek, none emigrated from Big Creek, suggesting physical barriers may be an effective management tool for reducing or preventing escapement. The results of this study demonstrate escapement is an important factor in regulating Walleye populations and can lead to greater fish loss than either harvest or natural mortality. Our model estimates also indicate Walleye harvest less on an effect on populations than natural mortality and escapement in systems without barriers; as natural mortality is difficult to manipulate, managers should focus on reducing escapement to mitigate the effect of natural mortality on Walleye densities. By understanding how different mechanisms regulate Walleye populations and how behavior is related to mortality sources, managers can focus efforts on the major sources of fish loss, leading to simplified management of Walleye populations and increased angling opportunities.

Acknowledgements

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Table 1. Akaike’s Information Criterion (AIC\textsubscript{c}), ΔAIC\textsubscript{c} (difference in AIC\textsubscript{c} values between the best model and other models), AIC\textsubscript{c} weight (W\textsubscript{i}), number of parameters (K), and deviance of multi-state models used to estimate weekly natural mortality (M), detection (p), harvest (Ψ\textsubscript{L-H}), and escapement (Ψ\textsubscript{L-E}) probabilities of adult Walleye in Big Creek and Brushy Creek lakes, Iowa, USA from October 2016 through May 2019. Effects included variation among time (t), lakes (L), years (Y), months (Mo), and water temperature (Tm). Models also included the effect of various water level metrics (maximum (Mx), minimum (Mn), average (Av), and coefficient of variation (CV)) for the week prior to tracking events.

<table>
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<th>Model</th>
<th>AIC\textsubscript{c}</th>
<th>ΔAIC\textsubscript{c}</th>
<th>W\textsubscript{i}</th>
<th>Model Likelihood</th>
<th>K</th>
<th>Deviance</th>
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<tr>
<td>Escapement (Ψ\textsubscript{L-E})</td>
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<td>M(Tm) p(L+Tm) Ψ(L-H(L+Mo(Apr-Jul))) L-E((Apr7dAv)))</td>
<td>6,882.52</td>
<td>0.00</td>
<td>0.44</td>
<td>1.00</td>
<td>11</td>
<td>6,860.25</td>
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<td>W&lt;sub&gt;i&lt;/sub&gt;</td>
<td>Model Likelihood</td>
<td>K</td>
<td>Deviance</td>
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<td>M(L+t) p(L+t) (\Psi(L-H(L+t) L-E(t)))</td>
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Figure 1. Location and outlines of Brushy Creek Lake (Webster County, IA; left) and Big Creek Lake (Polk County, IA, right) with spillway areas indicated by black stars.

Figure 2. Multi-state model diagram illustrating possible states for radio-tagged adult Walleye: in lake (L; Big Creek or Brushy Creek), escaped to the tailrace (E), or harvested by an angler (H), as well as survival (S), detection ($p$), and transition ($\Psi$) probabilities.

Figure 3. Weekly detection probabilities ($\pm$ 95% CI) as a function of water temperature (°C) for radio-tagged adult Walleye in Big Creek (grey) and Brushy Creek (black) lakes, Iowa, USA.

Figure 4. Weekly natural mortality probabilities ($\pm$ 95% CI) as a function of water temperature (°C) for adult Walleye in Big Creek and Brushy Creek lakes, Iowa, USA.

Figure 5. Weekly harvest probability estimates ($\pm$ 95% CI) for adult Walleye in Big Creek and Brushy Creek lakes, Iowa, USA from April-July versus the rest of the year.

Figure 6. Weekly escapement probability estimates ($\pm$ 95% CI) of adult Walleye from Brushy Creek, Iowa, USA as a function of mean water level (m) during April. Points represent observed values (n=12).

Figure 7. Relative effects of natural mortality (solid), harvest (dashed), and escapement (dotted) on a hypothetical population of adult Walleye in Big Creek (right) and Brushy Creek (left) as a function of month and year. Single lines represent the effect of an individual source of fish loss on the Walleye population.

Figure 8. Water depth at Walleye locations ($\pm$ 95% CI; top panel) and Walleye minimum weekly movement rate ($\pm$ 95% CI; bottom panel) in Big Creek and Brushy Creek lakes, Iowa, USA across
seasons. Differences in letters in the depth panel indicate differences among seasons. “N/A” is included in the movement rate panel, as infrequent tracking during winter did not allow for calculation of movement rates.

**Figure 9.** Mean depth, movement rate, and core and home range sizes of adult Walleye grouped by final fate in Big Creek and Brushy Creek lakes, Iowa, USA. “N/A” is included for groups where a parameter could not be estimated.
Figure 2.

Escapement (E)

$S = 0$
$p = 1$

Lake (L)

Big Creek, Brushy Creek

$S = ?$
$p = ?$

Harvest (H)

$S = 0$
$p = 0.75$

Big $\Psi^{L-E} = 0$
Brushy $\Psi^{L-E} = ?$

$\Psi^{E-L} = 0$

$\Psi^{H-L} = 0$

Big $\Psi^{L-H} = ?$
Brushy $\Psi^{L-H} = ?$
Figure 3.
Figure 4.
Figure 5.
Figure 6.
Figure 7.

Figure 8.
Figure 9.

Fish fate