Environmental Correlates of Walleye Spawning Movements in an Appalachian Hydropower Reservoir

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Abstract: Understanding walleye (*Sander vitreus*) spawning behavior is important for managing walleye fisheries, but such information is limited for Appalachian reservoirs. We assessed spawning movements and spawning locations for a reestablished walleye population in Cheat Lake, West Virginia. We tagged fifty-two walleye with acoustic telemetry transmitters to evaluate environmental correlates associated with pre-spawn movements and to determine spawning locations. Using an information-theoretic approach, we compared candidate logistic regression models to determine which environmental variables best explained upstream movements to spawning areas. The two models with the most support both included additive effects of year and water temperature, with sex also included in the second of these models. Water temperature had a significant positive relationship with pre-spawn movements in each model. Other environmental covariates such as river discharge and water elevation were not significant predictors of upstream pre-spawn movements. Walleye made pre-spawn upstream movements in late winter/early spring to spawning areas in the headwaters of Cheat Lake during periods of elevated water temperatures (75% of movement events occurred at water temperatures >4.1 C) where spawning occurred in shallow (<1.5 m), rocky habitat. Male walleye generally made upstream pre-spawn movements earlier than females. Our results also suggested the timing of walleye spawning with respect to water-level fluctuations could influence reproductive success due to stranding of eggs or reducing suitable spawning habitat. Knowledge of pre-spawn movement patterns and spawning locations could aid management of this recovering population. Benefits to management may include the prediction of spawning timing and locations for broodstock surveys and influences of water-level fluctuations and other environmental stressors on spawning success.

Key words: *Sander vitreus*, acoustic telemetry, spawning habitat, water level

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Walleye (*Sander vitreus*) is an economically important sportfish that requires specific habitat for successful spawning, often making large movements to reach spawning areas (Bozek et al. 2011b, Hayden et al. 2014, Raabe et al. 2020). Consequently, an understanding of spawning movements and locations is critical for management and conservation of this species (Bozek et al. 2011b, Matley et al. 2020). Knowledge of spawning movements and locations can help managers suitably regulate angler harvest on spawning aggregations to conserve walleye populations (Pritt et al. 2013, Bade et al. 2019, Matley et al. 2020). Also, the amount of suitable spawning habitat available can mediate successful reproduction (Bozek et al. 2011b, Raabe et al. 2020) and environmental stochasticity during spawning can likewise influence walleye recruitment (Hansen et al. 1998, Bozek et al. 2011b). Thus, knowledge of spawning movements and locations allows managers to determine if suitable spawning habitat exists and if environmental stressors or angler pressure may be influencing populations.

Walleye movement and habitat use varies among water bodies (Bozek et al. 2011b). Walleye often exhibit more frequent and longer movements during late winter and early spring in relation to spawning activity (Bozek et al. 2011a). Additionally, lake and reservoir walleye populations may spawn in lentic habitat and/or lotic habitat but are typically shallow water (30–75 cm) spawners (Bozek et al. 2011b, Raabe and Bozek 2012, Papenfuss et al. 2018). Environmental variables often associated with increased spawning movements include water temperature and river discharge (Paragamian 1989, Palmer et al. 2005, Bozek et al. 2011b, Pritt et al. 2013). Understanding stock-specific environmental cues for spawning movements can increase managers' ability to predict timing of spawning movements and identify spawning locations (Brooks et al. 2019). Numerous studies have been conducted on walleye movements and associated environmental correlates, with most focused on populations in the Laurentian Great Lakes (e.g., Hayden et al. 2014, Hayden et al. 2019, Matley et al. 2020, Elliot et al. 2022, McKee et al. 2022), as well as river systems and natural lakes within northern and midwestern states (e.g., Paragamian 1989, DePhilip et al. 2005, Bozek et al. 2011b). Comparatively few studies investigating possible environmental influences on walleye

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movement have been conducted in Appalachian reservoirs (Williams 2001, Palmer et al. 2005).

Cheat Lake is a hydropower reservoir in northern West Virginia supporting a walleye fishery that once was extirpated due to acidification within the watershed (Core 1959, Smith et al. 2022). Although walleye subsequently were reestablished within the reservoir, little has been known about their movement patterns and spawning locations. The lake also experiences seasonally varying fluctuations in water levels because of hydropower operations; impacts of these fluctuations on walleye spawning and spawning-related movements also have been unknown. Water-level fluctuations during spawning periods influence movements and can limit reproductive success of fish species (Rogers and Bergerson 1995, Jones and Rogers 1998, Paukert and Fisher 2000, Paukert and Fisher 2001), including walleye (Johnson 1961, Bozek et al. 2011b, Martin et al. 2012, Papenfuss et al. 2018). Additionally, water elevation changes during or after spawning may lead to reduced reproductive success through the stranding of eggs, or through limitation of suitable habitat (Hirsch et al. 2017, Papenfuss et al. 2018, Raabe et al. 2020). Although water-level changes have been shown to influence walleye spawning success, research is lacking on the potential influence of changing reservoir water levels on spawning movements. Therefore, the objectives of this study were to: 1) identify environmental cues associated with the movement of walleye to spawning areas; and 2) identify walleye spawning areas in Cheat Lake and how changing water levels may impact spawning in these areas.

Study Area

Cheat Lake was created in 1926 by the damming of the Cheat River near the West Virginia-Pennsylvania border for hydroelectric generation. The 700-ha reservoir extends 21 km from the dam to the first upstream exposed riffle and has a maximum depth of 24 m near the dam. Acid precipitation and acid mine drainage from abandoned mine lands degraded water quality of the Cheat River watershed for over a century (Core 1959, Freund and Petty 2007, Merovich et al. 2007). In recent years, the water quality of the Cheat River watershed and Cheat Lake have substantially improved due to mitigation efforts throughout the watershed (Thorne and Pitzer 2004, McClurg et al. 2007, Smith et al. 2022). In response to improved water-quality conditions, walleye were reestablished in Cheat Lake through West Virginia Division of Natural Resources (WVDNR) reintroduction efforts beginning in 2001 (Smith et al. 2022). Reservoir water levels fluctuate seasonally due to hydropower operations, with a 4-m difference between full pool (summer) and minimum winter pool (Matt et al. 2021). The reservoir is operated so that water levels are no less than 2.1 m below full pool in April to facilitate successful spawning of walleye and yellow perch (*Perca flavescens*; Hilling et al. 2018), and so that levels from May to October are no less than 0.6 m below full pool (Matt et al. 2021).

Methods

Fish Collection and Tagging

Fifty-two walleye (432–708 mm TL; 30 males, 20 females, 2 undetermined) were collected from late October–early February during 2011–2013 using either pulsed, direct current (150–350 V; 6 amps; 60 Hz) boat electrofishing (type 5.0 GPP, Smith-Root, Inc., Vancouver, Washington) or gill nets (experimental nets, 45 m long, 1.8 m deep, with alternating 7.6-m panels of 25-, 38-, and 51-mm bar mesh). Prior to surgery, walleye were measured (TL, mm), weighed (g), anesthetized using a MS-222 solution (tricaine methanesulfonate; 100 mg L^{-1}), and affixed with an external anchor tag with printed text asking anglers to release these fish if caught. An acoustic transmitter (Sonotronics coded temperature transmitters [Sonotronics, Inc., Tucson, Arizona]; CTT-83-3-I, 62 mm length, 16 mm diameter, 10 g in water, 3-year battery life) was surgically implanted into the abdominal cavity of each walleye through an incision of approximately 20–30 mm (Hart and Summerfelt 1975). Approximately 3–4 sutures of non-absorbable monofilament were used to close the incision. Surgical procedures never exceeded 7 min and fish gills were irrigated continuously with lake water. Walleye were sexed during surgery by examination of the gonads through the surgical incision or by the expression of milt for males. After surgery, fish were allowed to fully recover before release. Transmitter weight was ≤2% of each fish's weight (Winter 1996).

Telemetry and Environmental Data Collection

Walleye locations and movements were monitored primarily with fixed location telemetry via stationary receivers. Sonotronics submersible underwater receivers (SUR) were deployed at eleven fixed locations throughout Cheat Lake (Figure 1). Some supplementary tracking was conducted manually using a handheld acoustic hydrophone, primarily to determine specific spawning areas utilized by telemetered fish. To aid in determination of the onset of the walleye spawning migration, we subdivided Cheat Lake into two zones: the main lake (including embayments) and the upstream riverine section (Figure 1). Demarcation of these zones was based on limnological and habitat differences between these areas as well as on results from previous analyses of walleye distribution in Cheat Lake, where individuals typically overwinter downstream of the riverine zone (Smith et al. 2021).

We examined four environmental covariates with walleye movement: water elevation, incoming river water temperature, lunar phase, and river discharge. Mean daily river discharge (m^3 sec^{-1}),

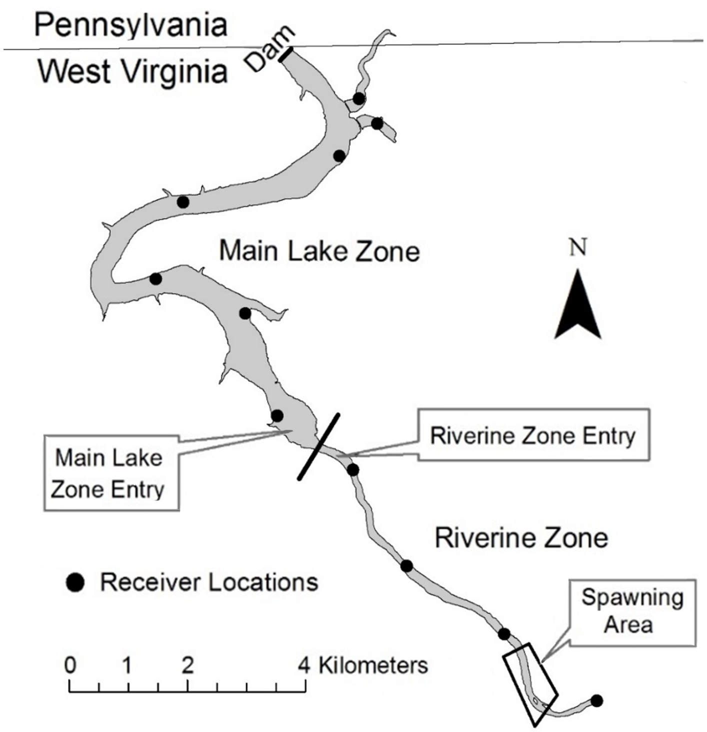

Figure 1. Study site map showing location of acoustic receivers, separation of main lake zone and riverine zone (represented by black bar in between two entry points), and location of walleye spawning area in Cheat Lake, West Virginia.

water elevation (m above sea level), and incoming river water temperature (C) were acquired from the U.S. Geological Survey (USGS; http://water.usgs.gov/waterwatch). Specifically, the river discharge and water temperature data were acquired from a USGS stream gage on the Cheat River at Albright, West Virginia (USGS streamgage 03070260), approximately 24 rkm upstream from the head of Cheat Lake. Water-elevation data were from the Lake Lynn hydropower station on Cheat Lake (USGS streamgage 03071590). Lunar phase data were acquired from the U.S. Naval Observatory (http://www.usno.navy.mil/USNO/astronomical-applications) and consisted of a daily lunar index of the illuminated percentage of the moon face ranging from 0 (new moon) to 1 (full moon).

Data Analysis

Data from stationary receivers were processed using the Sonotronics software SURsoftDPC. False detections are possible with acoustic telemetry and may occur due to background noise or when multiple fish are close to the hydrophone (Clements et al. 2005). We removed erroneous data by omitting detections that occurred only once within a 24-h period or by eliminating records when fish were detected as being in separate locations simultaneously (Ramsden et al. 2017).

Spring fisheries surveys and angler reports suggested that most Cheat Lake walleye appeared to spawn in the riverine zone. This was confirmed by yearly movements of study fish from the main lake zone to the riverine zone in the weeks prior to suitable spawning conditions (Smith et al. 2021). Therefore, our analysis of environmental covariates associated with upstream movements to the spawning grounds was based on modeling the direct movements of telemetered study fish from the main lake zone into the riverine zone under the assumption that these movements were correlated with pre-spawn behavior. Only walleye that made upstream movements were included in data analyses. Additionally, walleye with a core range (encompassing 50% of receiver areas detected) that included the upstream riverine zone were excluded from analyses. We assessed walleye upstream movements and associated environmental covariates during the period from 1 January to the date of final upstream movement for each individual prior to spawning. For analysis of upstream movements, we assigned a binomial response (1 = movement upstream, 0 = no movement upstream) for each walleye each day prior to final initiation of upstream movement. Initiation of upstream movement was considered when an individual fish first entered the riverine zone of Cheat Lake and continued upstream, signaling departure from their overwintering locations in the main lake zone.

We modeled upstream movement in relation to environmental covariates using binomial generalized linear mixed models (GLMM) with PROC GLIMMIX in SAS (Littell et al. 2006, SAS 2013), a common approach to model probability of fish movement or migration (Henderson et al. 2014, Amtstaetter et al. 2015, Eyler et al. 2016). Examined covariates included year, sex, and environmental variables (water temperature, log-transformed river discharge, water elevation, lunar phase) as fixed effects. Individual fish were included as random effects to account for repeated measures on each fish (Rogers and White 2007).

Given the large number of potential models that could be developed with this set of covariates, we focused on a smaller set of candidate models developed based on published literature of fish movement (Paragamian 1989, Williams 2001, DePhilip et al. 2005, Bozek et al. 2011b). Candidate models included a full model (effects of year, sex, water elevation, water temperature, river discharge, and lunar phase), single variable and two variable additive models of sex and/or environmental covariates both with and without a year effect, and an intercept-only model with no predictor variables. The candidate models were ranked by Bayesian Information Criterion (BIC) in SAS (SAS 2013), as BIC has been shown to be appropriate for models with large sample sizes and more robust to model overfitting than other criteria (Aho et al. 2014). The model with the lowest BIC score was considered as the best fitting model (Burnham and Anderson 2004). However, all models with ΔBIC values < 2 were considered competing models; our decision on which models and included covariates may have best explained the data was based on this threshold (Burnham and Anderson 2004).

Prior to analysis we assessed multicollinearity using Pearson's correlation coefficient and the variance inflation factor (VIF) to determine if it was necessary to remove any covariates from our models due to high correlation with other covariates. The VIF was calculated for the full model in SAS. A value greater than 10 would suggest considerable collinearity (O'Brien 2007). Pearson's correlation coefficients for variables in the full model were calculated, with correlation > 0.7 indicating potential collinearity and possibly redundant variables (Dormann et al. 2013).

Results

A total of 31 walleye (18 males; 13 females) made upstream movements during the pre-spawn periods of 2012–2015 and were used for data analyses. The earliest upstream movements occurred in February in all years except 2013, when the earliest movement event occurred on 13 January (Figure 2). The latest upstream movements occurred on 4 April in both 2013 and 2014 (Figure 2). Number of days with upstream movement events ranged from 7 days in 2012 to 17 days in 2013 (Figure 2). Two walleye (one male and one unsexed fish) were excluded from analysis of upstream movement due to their core range encompassing the spawning area, eliminating the occurrence of pre-spawn movement events. An additional six walleye were excluded from analysis due to their lack of an upstream movement from the main lake zone to the riverine spawning grounds. An additional thirteen walleye (including the second unsexed fish) did not provide data on upstream movements due to mortality from unknown causes, downstream dam passage, or transmitter failure prior to the spawning season.

Walleye made upstream pre-spawn movements during a wide range of environmental conditions, including both high and low river discharge (47.9–577.7 m^3 sec^{-1}) and water elevation levels (261.6–265.2 m above sea level; Table 1). Upstream movement

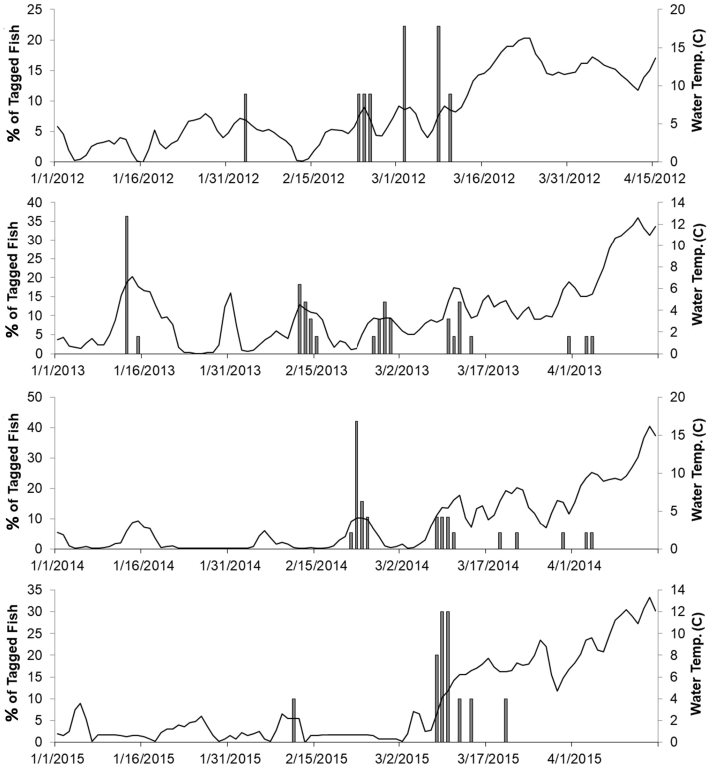

Figure 2. Daily percentage of tagged walleye migrating into the riverine zone (gray bars) in Cheat Lake, West Virginia and associated water temperature (black line) data for 2012–2015.

Table 1. Summary statistics of three environmental variables (mean daily water elevation, mean daily river discharge, and mean daily water temperature) during days of upstream pre-spawn migration and days without upstream pre-spawn migration for walleye in Cheat Lake, West Virginia.

	Water elevation (m above sea level)		**River discharge (m^3 s^{-1})**		**Water temperature (C)**	
Year	**Mean (95% CI)**	**Range**	**Mean (95% CI)**	**Range**	**Mean (95% CI)**	**Range**
Days with upstream pre-spawn movement						
2012	263.2 (262.3–264.2)	261.6–264.8	126.7 (40.3–213.1)	53.2–317.1	6.3 (5.7–6.9)	5.5–7.2
2013	264.1 (263.7–264.6)	262.5–265.1	132.9 (93.5–172.2)	47.9–302.9	4.7 (4.0–5.4)	3.2–6.6
2014	263.9 (263.3–264.5)	262.3–265.2	145.0 (86.3–203.7)	60.6–379.5	5.9 (4.7–7.2)	3.6–10.1
2015	264.4 (263.7–265.1)	263.2–265.1	232.3 (66.0–398.5)	107.0–577.7	4.7 (3.0–6.4)	2.2–6.6
All	263.9 (263.7–264.3)	261.6–265.2	151.3 (118.2–184.4)	47.9–577.7	5.3 (4.8–5.9)	2.2–10.1
Days without upstream pre-spawn movement						
2012	264.0 (263.8–264.3)	261.6–265.1	113.7 (80.1–147.2)	30.6–656.9	4.2 (3.7–4.8)	0.1–7.3
2013	263.9 (263.7–264.0)	262.5–265.1	108.7 (83.1–134.6)	29.2–699.4	2.6 (2.2–3.0)	0–7.1
2014	263.1 (262.9–263.3)	261.9–265.2	86.7 (71.3–102.0)	18.8–413.4	1.9 (1.4–2.4)	0.1–10.1
2015	263.8 (263.5–263.9)	262.0–265.1	116.9 (78.3–155.5)	33.1–880.7	1.5 (1.1–1.9)	0–7.7
All	263.6 (263.5–263.7)	261.6–265.2	105.1 (90.9–119.2)	18.8–880.7	2.3 (2.0–2.6)	0–10.1

events were more likely to occur during periods when water temperatures were warmer than average (Table 1, Figure 2). Upstream movement occurred at a range of water temperatures (2.2–10.1 C), but 75% of upstream movement events occurred at water temperatures >4.1 C.

Multicollinearity did not significantly affect our model performance, as our full model had a VIF less than 2 and all variable pairwise correlation coefficients were less than 0.5. The GLMM analysis supported two different additive-effects models, one including effects of year and water temperature (ΔBIC = 0) and the second including effects of year, water temperature, and sex (ΔBIC = 0.53). Both models had positive coefficients for water temperature (Table 2), indicating that pre-spawn upstream movement events were associated with elevated water temperatures. Upstream movements were almost always concentrated around spikes in water temperature although there were also incidences of temperature spikes with no upstream movement (Figure 2). Mean water temperature during upstream movement events each year was always greater than mean water temperature during non-movement (Table 1). Additionally, in the ranking of candidate models the top 10 models all included water temperature. Upstream movements of females typically occurred later than those of males. Most (68.9 %) male walleye moved upstream prior to March, with fewer moving in March (28.9 %) or April (2.2 %). In contrast, fewer (39.5 %) females moved upstream prior to March, most moved upstream in March (52.6 %), and the least in April (7.9 %). Models that included water elevation, river discharge, and lunar phase were not supported.

Upstream movement of walleye was occasionally interrupted, resulting in temporary return to the main lake. In all cases, these fish eventually returned upstream and reached the spawning grounds prior to spawning. In total, 13 fish (7 males; 6 females) exhibited such fallback to the main lake and subsequently returned upstream prior to spawning. Additionally, three of these fish (1 male; 2 females) had two instances each of fallback into the main lake before returning upstream to spawn. Fallback events were observed for 0 fish in 2012, 9 in 2013, 5 in 2014, and 2 in 2015. Fallback usually occurred during periods of low water temperatures, specifically when water temperatures cooled substantially after a period of warm water temperatures. Mean water temperatures were lower during downstream fallback movements ($\bar{x}$ = 1.8, SE = 0.5 C) compared to mean water temperatures during no downstream fallback movement ($\bar{x}$ = 3.6, SE = 0.2 C). Most of these downstream fallback movements occurred when water temperature was near freezing (i.e., <1 C).

Table 2. Parameter estimates for the two best-fitting logistic regression models from Bayesian Information Criterion model selection (ΔBIC < 2) using environmental variables to describe upstream pre-spawn migration of walleye in Cheat Lake, West Virginia from 2012–2015. Intercept term is for Year = 2015 in the first model (top) and for Sex = Male and Year = 2015 in the second model (below).

Parameter	Estimate	SE	*t* statistic[a]	*P*
Model 1 (ΔBIC = 0.00)				
Intercept	–5.84	0.44	–13.3	< 0.001
Year 2012	–2.34	0.62	–3.8	<0.001
Year 2013	–1.19	0.44	–2.8	0.008
Year 2014	–0.36	0.42	–0.9	0.395
Water temperature	0.83	0.08	10.8	< 0.001
Model 2 (ΔBIC = 0.53)				
Intercept	–5.43	0.47	–11.5	< 0.001
Year 2012	–2.65	0.64	–4.1	< 0.001
Year 2013	–1.41	0.46	–3.0	0.002
Year 2014	–0.49	0.42	–1.1	0.249
Sex (Female)	–0.64	0.37	–1.7	0.084
Water temperature	0.85	0.08	10.8	< 0.001

a. df = 30 for intercepts; 3546 for each other coefficient in Model 1; 3545 for each other coefficient in Model 2.

Discussion

Pre-spawn upstream movements of walleye in Cheat Lake were driven primarily by water temperature, with walleye more likely to initiate upstream movement towards spawning areas during periods of higher water temperatures. Conversely, other environmental factors (i.e., river discharge, water elevation, etc.) were not supported as being significant predictors of walleye pre-spawn movements. Studies on walleye movements have previously suggested that pre-spawn movement is correlated with warming water temperatures (Paragamian 1989, Pitlo 1989, Bellgraph et al. 2008, Bozek et al. 2011b). Our data suggest that walleye in Cheat Lake typically begin upstream movement when water temperatures are on average >4 C. However, a wide range of water temperatures have been associated with migration (Bozek et al. 2011b) and temperatures at which upstream movement occurred in Cheat Lake varied among individuals. The only upstream movements observed at water temperatures <3 C occurred in 2015 when water temperatures remained near freezing for most of the pre-spawn period. These movements took place during slightly warmer water temperatures in February and early March. Similarly, Bozek et al. (2011b) noted a delay in spawning after arriving at spawning shoals if water temperatures were unsuitably low.

Though some females consistently moved upstream as early as males, on average males moved upstream earlier, suggesting that sex influences upstream movements. This difference between sexes is similar to what has been reported in other studies, and researchers generally believe that early arrival allows male walleye to increase their reproductive opportunity with females by remaining near spawning areas for a longer period (Hayden et al. 2014, Raby et al. 2018, Bade et al. 2019). Sex-based differences in spawning movements have also been observed in other species such as some salmonids, sturgeon, and some marine species (Morgan and Trippel 1996, Morbey 2000, Dammerman et al. 2019, Baril and Magnan 2022). Sex-specific differences in pre-spawn movements could bias stock assessment surveys and angler exploitation, as females usually grow faster and larger than males (Pritt et al. 2013, Brooks et al. 2019, Elliott et al. 2022). Additionally, increased time spent by males near spawning areas could skew angler catch rates of male fish, as noted by Bade et al. (2019). However, females that spend substantial time near spawning areas are likewise subjected to increased vulnerability to angling (Palmer et al. 2005, Bade et al. 2019).

Some walleye temporarily left spawning areas after arriving and moved back downstream to the main lake when water temperatures decreased sharply prior to spawning. These events resemble a phenomenon termed "fallback" in movement studies of other species (Naughton et al. 2006, Frank et al. 2009). Fallback commonly has been observed in anadromous salmonid species (Reischel and Bjorn 2003, Naughton et al. 2006, Frechette et al. 2020), but it has also been documented in freshwater migratory species (McLaughlin et al. 2013, Harper et al. 2018). Fallback events have been attributed to increased flow, reduced water clarity, and sudden changes in water temperature (Reischel and Bjornn 2003, Boggs et al. 2004, Naughton et al. 2006). Fallback has not been previously observed for walleye, although Bozek et al. (2011b) noted a delay in spawning after arriving at spawning shoals if water temperatures were unsuitably low. In our study, fallback events nearly always occurred during periods of decreasing water temperatures. In all cases, fish that displayed fallback and left spawning areas early eventually returned to spawning grounds when water temperatures warmed. Management implications of fallback occurrence for Cheat Lake walleye are unknown, but other studies have suggested that fallback may lead to reduced spawning success or pre-spawn mortality (Reischel and Bjornn 2002, Naughton et al. 2006, Frank et al. 2009, McLaughlin et al. 2013). Spawning success of telemetered walleye was not determined in this study but no telemetered fish that exhibited fallback suffered pre-spawn mortality.

Lake level was not supported as a predictor of upstream movement, but it could nevertheless have important consequences during the spawning period. Telemetry results and concurrent fishery survey data suggest that many Cheat Lake walleye spawn in shallow (<1.5 m), rocky shoal areas near the head of the reservoir from mid-March to early April, depending on water temperature. This area of the reservoir is impacted by water-level fluctuations in early spring, which could lead to egg stranding if reservoir levels suddenly decrease after spawning. In examining fluctuations of lake levels during periods of estimated spawning activity, the maximum decrease in water elevation during the telemetry study occurred during 2014, when water elevation decreased by 2 m over a 72-h period. In comparison, the maximum decreases in water elevation during spawning periods in 2012, 2013, and 2015 were 0.6 m, 1.7 m, and 1.7 m respectively. In years since the telemetry study (2016–2022), maximum water elevation decreases during the spawning period (11 March – 12 April) ranged from 0.91 – 2.57 m, averaging 1.73 m. Studies on yellow perch in Cheat Lake reported dewatered eggs following reservoir drawdown events (Hilling et al. 2018, Matt et al. 2021). Several studies have suggested the potential for decreasing water levels to lead to egg and larval mortality in walleye (Johnson 1961, Chevalier 1977, Bozek et al. 2011b).

Understanding timing and location of walleye spawning could allow managers to better predict potential impacts of fluctuating lake levels and other environmental stressors on spawning success. In Cheat Lake, water elevation restrictions change from maximum drawdown (4.0 m) to a restricted drawdown (2.1 m) on 1 April of each year (Matt et al. 2021). This restriction is designed to facilitate successful spawning conditions and increase spawning habitat for walleye (Matt et al. 2021). However, our study suggests that walleye spawning likely occurs as early as mid-March, especially in warmer years. Furthermore, walleye spawning may increasingly occur earlier due to the potential future impacts of climate change (Schneider et al. 2010). Therefore, the fluctuation restriction on 1 April may provide little benefit, especially during warm years. Decreasing water levels could also reduce available suitable spawning habitat for walleye (Bozek et al. 2011b, Martin et al. 2012, Papenfuss et al. 2018, Raabe et al. 2020). Likewise, our manual tracking and night-time boat electrofishing surveys typically found walleye in suspected spawning areas to be in water less than 1.5 m deep, similar to results found in other studies (Johnson 1961, Raabe and Bozek 2012, Papenfuss et al. 2018). Given the likely spawning of individuals in water less than 1.5 m deep, the 2.1-m restriction may not provide complete protection from stranding should spawning occur at or near full pool. Ideally, future studies could quantify egg depositional areas and any associated influences of water-level fluctuations.

Understanding of how environmental conditions influence movements of walleye can improve the management of walleye harvest during the spawning period (Williams 2001, Rasmussen et al. 2002, Palmer et al. 2005). Although our data were limited to 31 telemetered walleye within a single reservoir, the results still provide valuable stock-specific information for managers and contribute to the overall body of literature on walleye movement behavior. Knowledge of timing and cues to pre-spawn migration could allow managers to better predict when upstream migration events are likely to occur and thus potentially inform regulatory action aimed at protecting spawning individuals from fishing mortality (Williams 2001, Bade et al. 2019). Anglers often target spawning aggregations which could influence reproductive success and adult abundance (Palmer et al. 2005). Results of our study can allow managers to evaluate the potential for overexploitation of walleye by anglers during the spawning period and take regulatory action if warranted. Also, knowledge of spatiotemporal aggregations could benefit spawning population monitoring programs by directing spawning stock surveys (Brooks et al. 2019). Ultimately, this increased knowledge of walleye movement and locations during this critical period could help ensure continued success of the reestablished Cheat Lake population.

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