Notes

Seasonal and Spatial Distribution of Walleye Sex Ratios in a Large Nebraska Reservoir

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Abstract

The ratio of female to male Walleye *Sander vitreus* across the spatial scale of large reservoirs and during nonspawning times receives little attention, even though standardized sampling occurs during this time. This study evaluated whether the proportion of female Walleye collected from seasonal sampling at different spatial areas within a large reservoir fell within the 0.450–0.550 range, which would closely reflect a 1:1 female-to-male sex ratio. We used a Bayesian generalized linear mixed-effects model with a binomial probability distribution to assess the proportion of female Walleye, using season (spring and fall) and reservoir zone (riverine, transitional, and lacustrine) as fixed effects and year (2015 and 2016) as a random effect. We collected a total of 2,163 Walleye using standardized Nebraska Game and Parks Commission gill-netting methodology and determined sex on a random subsample of fish ($n = 989$) collected throughout each reservoir zone. There was no meaningful deviation from the 0.450–0.550 range in the mean posterior estimate of the proportion of female Walleye caught in the riverine and transitional zones during either spring or fall. The mean (SD) posterior estimate of the proportion of female Walleye in the lacustrine zone was 0.182 (0.024) in the spring and 0.621 (0.032) in the fall. These results are consistent with previous observations of increased male presence near spawning locations in the spring and demonstrate that increased fall female catch in the lacustrine zone could potentially bias sampling results. This study provides further insight into the distribution of sexes across the spatial gradient of a large Great Plains reservoir and demonstrates a need to sex Walleye during standardized fall surveys.

Keywords: sex ratio; walleye; reservoir; season; Bayesian

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Introduction

Walleye *Sander vitreus* is an important recreational species throughout its native and introduced range and is among the most commonly sought species by anglers in northern inland waters of the United States (Schmalz et al. 2011). As a result, Walleye populations can be subject to substantial levels of exploitation (Quist et al. 2010a, 2010b; Blackwell et al. 2019) that can directly affect their population characteristics (Sass and Shaw 2018; Blackwell et al. 2019). To counteract this high exploitation, Walleye populations in Great Plains reservoirs are commonly maintained through stocking efforts (Porath et al. 2003; Olson et al. 2007; Quist et al. 2010b) and regulations to prevent overharvest (Quist et al. 2010a; Spink 2012; Koupal et al. 2015).

Walleye populations in large reservoirs are known to exhibit spatial and temporal variability in multiple population metrics such as size, age structure, and relative abundance (Hubert and O'Shea 1992; Palmer et al. 2005; Schall et al. 2019, 2021). Differences in Walleye distribution are commonly associated with seasonal behaviors and can vary between sexes. In particular, Walleye are known to exhibit distinct spatial segregation during spawning periods, such as differential movement patterns and habitat preferences among subpopulations and sexes (Palmer et al. 2005; Bade et al. 2019). Sex ratios of samples collected during the spawning season in presumed spawning locations typically skew toward males (Colby et al. 1979; Koupal et al. 1997), which tend to arrive earlier and remain longer at spawning locations (Rawson 1957; Wang et al. 2007; Bade et al. 2019), but samples can return to an approximately 1:1 ratio by as early as late spring (Pritt et al. 2013). In large lentic systems, large adult Walleye commonly move offshore during summer and fall to deeper, cooler water in search of thermal refuge or to forage on schools of pelagic prey (Rawson 1957; Bowlby and Hoyle 2011; Hayden et al. 2014). Female Walleye often make these offshore movements earlier than males (Raby et al. 2018), which may influence the sex ratio in the deeper, lacustrine zone and partially explain the higher female proportion observed in the fall.

Understanding how sex ratios change throughout the sampling season and across the spatial scale of large reservoirs can be important for interpreting targeted sampling results of Walleye populations. During the spring in large Great Plains reservoirs, male-biased capture ratios would be anticipated from samples occurring during spawning time at spawning locations (Grinstead 1971; Katt et al. 2011; Martin et al. 2012). However, the impact of sex-related characteristics and differences on fisheries research and management is often understudied and overlooked (Hanson et al. 2008), and limited information is known about sex ratios of sampled Walleye in other areas of these reservoirs and at other times beyond sampling during the spawning season near known spawning sites. Standardized sampling of Walleye in Great Plains reservoirs typically occurs in the fall (Zuerlein and Taylor 1985; Miranda and Boxrucker 2009), and sex composition in standardized samples of species exhibiting sexual size dimorphism can strongly influence estimates of population metrics, such as age and size structure (Colvin 2002). Also, variation in sex ratios of sexually size-dimorphic species can influence angler harvest (Schoenebeck and Brown 2011; Myers et al. 2014). To better understand how sex ratios change over time and across the reservoir spatial scale, this study evaluated Walleye sex ratios in spring and fall in three zones within a large Great Plains reservoir. The primary objective was to determine if the proportion of female Walleye differed from males in gill-net samples collected at varying seasonal and spatial scales in Lake McConaughy, Nebraska.

Methods

Study site

Lake McConaughy is a flood-control and irrigation reservoir located in southwestern Nebraska and was created by the construction of Kingsley Dam on the North Platte River (Figure 1). The reservoir covers 14,164 ha, has maximum and mean depths of 53 and 22 m, and extends approximately 35 km at full pool (Taylor and Hams 1981). Lake McConaughy consistently has the highest angling pressure among Nebraska reservoirs (Chizinski et al. 2014), and Walleye is the primary species sought by anglers (Porath et al. 2003). As in other Great Plains reservoirs (Katt et al. 2011), Walleye spawning in Lake McConaughy is known to be concentrated along the dam, but the extent of spawning up-reservoir is not well documented. Additionally, the Walleye population in Lake McConaughy has been supplemented by near-annual stockings since 1989 (Porath et al. 2003; Perrion 2016).

Sampling

We sampled Walleye using overnight-set, experimental monofilament gill nets in spring (May) and fall (September) during 2015 and 2016 (Data S1,*Supplemental Material*). Gill nets measured 45.7 m long and 1.8 m deep and were composed of six 7.6-m-long panels with bar mesh sizes arranged in the following order: 19.1, 25.4, 31.8, 38.1, 50.8, and 76.2 mm. On the basis of standard Nebraska Game and Parks Commission protocol (Zuerlein and Taylor 1985), we set gill nets perpendicular to shore with the small mesh end nearshore at a depth of 2–3 m. We set gill nets in the evening and retrieved them the following morning. Mean (SD) soak times for overnight gill-net sets in spring and fall were 12.8 (1.6) and 13.6 (1.3) h. To evaluate the spatial distribution of sex ratios, we divided the reservoir into three equal-sized zones approximately 8 km in length and distributed sampling effort equally among three reservoir zones: riverine, transition, and lacustrine (Figure 1). Within each sampling zone, we divided north and south shorelines into 0.5-km subunits. We annually set a total of 36 gill nets during each sampling season, with 12 gill nets set in each zone. We divided effort equally among shorelines ($n = 6$ nets/shoreline) and set the nets in randomly selected

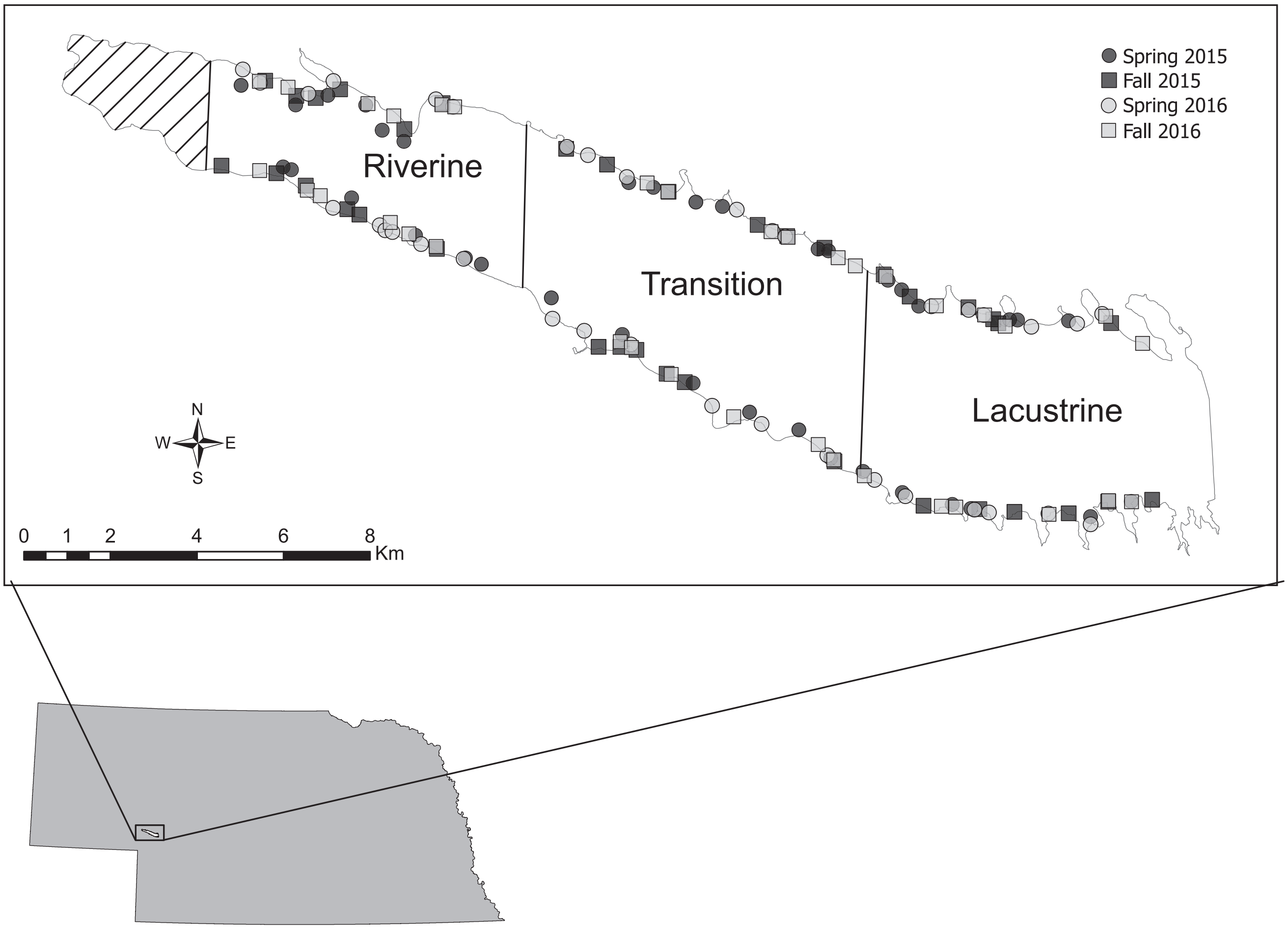

Figure 1. Map of Lake McConaughy, Nebraska, showing the sampling locations from spring and fall 2015 and 2016 distributed among the three reservoir zones (riverine, transition, and lacustrine) used to assess the proportion of females among the total Walleye *Sander vitreus* catch of overnight gill nets. The upper portion of the reservoir covered by the angled lines was not sampled during this study.

subunits without replacement. Therefore, over the 2 y of this study, we set a total of 24 gill nets per zone during each season. We recorded total length and sex on a random subsample of Walleye by visually observing gonads in the field from mortalities recovered in the gill nets. We returned all live fish to the reservoir and did not record sex, since male expression of gametes during the spring spawning period likely occurs over a longer time frame and could influence our estimates. Only fish considered fully recruited to the gill nets (≥200 mm; Shoup and Ryswyk 2016) were sexed. We assumed that that there was an equal probability of mortality by sex and total length of fish.

Analysis

We used a Bayesian generalized linear mixed-effects model to estimate the proportion of female Walleye across seasons and reservoir zones. We used reservoir zone and season as fixed effects and sampling year as a random effect, and we fit the model using a binomial probability distribution with a logit link. We determined prior inputs by using prior predictive simulation (Table 1; Wesner and Pomeranz 2021). We fit the model in rstan (Stan Development Team 2021) using a Hamiltonian Monte Carlo approach (Monnahan et al. 2017) with the brms package (Bürkner 2017) in program R (R Core Team 2021). The Hamiltonian Monte Carlo algorithm used four Markov chains, 2,000 iterations per chain, and a 1,000-iteration warm-up phase. We assessed model fit using posterior predictive checks and considered model convergence if Gelman–Rubin statistics were ≤1.1 (Brooks and Gelman 1998).

Table 1. Prior values for the three generalized linear mixed-effects models (base = base model; over 400 = model only including fish >400 mm; prior = model utilizing broader priors) assessing the proportion of female Walleye *Sander vitreus* caught in seasonal gill-net samples during two seasons (spring and fall) in Lake McConaughy, Nebraska, during 2015 and 2016.

Parameter	Base	Over 400	Prior
Intercept	*N*(0, 0.5)	*N*(0, 0.5)	*N*(0, 5)
β	*N*(0, 0.5)	*N*(0, 0.5)	*N*(0, 5)
$\beta_{\mathrm{Zone3} \times \mathrm{Season}}$	*N*(−1.5, 0.6)	*N*(−1.5, 0.6)	*N*(0, 5)
Σ	Exponential(25)	Exponential(25)	Exponential(10)

Table 2. Sample sizes of Walleye *Sander vitreus* collected across three reservoir zones (riverine, transitional, and lacustrine) in Lake McConaughy, Nebraska, during spring and fall 2015 and 2016. N_{base} = total number of Walleye ≥200 mm sampled in gill nets; n_{base} = number of fish ≥200 mm where sex was identified; N_{400} = total number of Walleye >400 mm sampled in gill nets; n_{400} = number of fish >400 mm where sex was identified.

Season	Zone	N_{base}	n_{base}	N_{400}	n_{400}
Spring	Riverine	206	116	81	68
	Transitional	248	144	97	81
	Lacustrine	443	238	242	139
Fall	Riverine	303	124	55	55
	Transitional	440	164	63	63
	Lacustrine	523	203	103	103

To evaluate the proportions of female Walleye in each reservoir zone by season, we calculated values as the inversive-logit transformed posterior estimates. We summarized mean proportions for each season and calculated 95% credible interval estimates for each. We calculated the probability that the proportion of female Walleye was between 0.450 and 0.550 because we wanted to determine if the sex ratios were close to 1:1. We assumed that natural variation from a 1:1 female-to-male sex ratio was likely and, therefore, provided a small range for the estimated proportion of females. We considered differences to be meaningful when the probability was <10.00% that the proportion of females was within the proposed range. To calculate probabilities, we simulated 8,000 iterations from the posterior distribution using a total catch value of 100 fish and calculated probabilities for each season and reservoir zone combination by dividing the sum of the number posterior iterations where the estimated number of females was ≥45 and ≤55 by the number of iterations.

We also performed sensitivity analysis to determine the influence of either the size of Walleye included in our model or of the priors in our base model described above. We fit a second model (hereafter the over-400 model) using only fish >400 mm in length to determine if there was any influence of sexual immaturity on our results. Walleye in Nebraska reservoirs have been shown to mature between 3 and 5 y of age (Spink 2012), so we selected 400 mm as the minimum size because nearly all Walleye >400 mm in Lake McConaughy were at least 3 y of age (Schall et al. 2021). We used the same modeling process and prior inputs as described above to fit this model. We then fit a third model (hereafter called the prior model) using all fish ≥200 mm and set broader priors to determine the influence of prior selection on the posterior estimates. Prior inputs for all models are listed in Table 1.

Results

We caught a total of 2,163 Walleye over 2 y and determined the sex of 989 individuals ($n_{females} = 441$, $n_{males} = 548$; Table 2). Mean (SE) total lengths of female

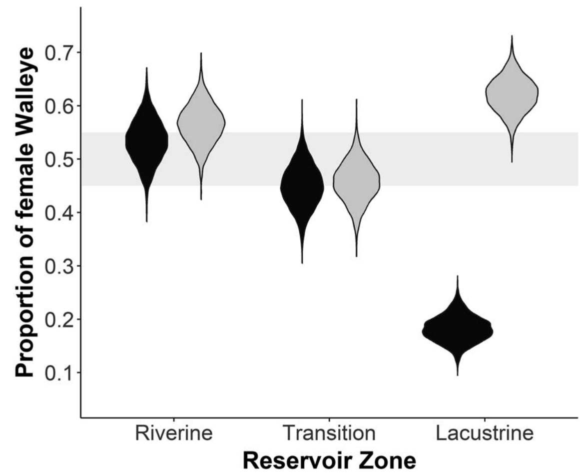

Figure 2. Violin plots of estimated posterior distributions derived from a generalized linear mixed-effects model (base model) of the mean proportion of female Walleye *Sander vitreus* among three reservoir zones (riverine, transition, and lacustrine) sampled during spring (black) and fall (gray) in Lake McConaughy, Nebraska, that used data collected in spring and fall 2015 and 2016. The light-gray shaded rectangle indicates the 0.450–0.550 range.

and male Walleye were 436 (5.9) mm and 418 (4.5) mm. We determined the sex of 58.2% of all sampled fish in 2015 and 36.9% of the total number sampled in 2016. The over-400 model included a total of 509 Walleye, of which 232 were females (Table 2).

The estimated mean (SD) proportion of female Walleye from the base model's posterior predictive distribution collected in the riverine and transitional zones of the reservoir ranged from 0.450 (0.040) to 0.566 (0.037). Estimated 95% credible interval ranges overlapped with the 0.450–0.550 range in both spring and fall in the riverine and transition zones (Figure 2). The probability that the proportion of females was within the 0.450–0.550 range in the riverine zone was 63.28% in the spring and 32.98% in the fall, and the probability in the transitional zone was 48.60% in the spring and 57.14% in the fall. In the lacustrine zone, the estimated mean (SD) proportion of females from the posterior predictive distribution was 0.182 (0.024) in the spring and 0.621 (0.032) in the fall, and there was no overlap of the 95% credible intervals with the 0.450–0.550 range in either season (Figure 2). The probabilities that the proportion of females in the lacustrine zone fell between 0.450 and 0.550 in the spring and fall were <0.01 and 0.02%, respectively.

Results of the sensitivity analysis indicated that the inclusion of immature fish and use of narrow priors in the base model had limited impact on the posterior estimates of the proportion of females across seasons and zones. On the basis of the over-400 model, the estimated mean (SD) proportion of female Walleye in the spring riverine zone increased to 0.613 (0.050), and all other proportions were within 0.033 of the base model (Figure 3). All probabilities that the estimated proportions in the riverine and transitional zones fell between

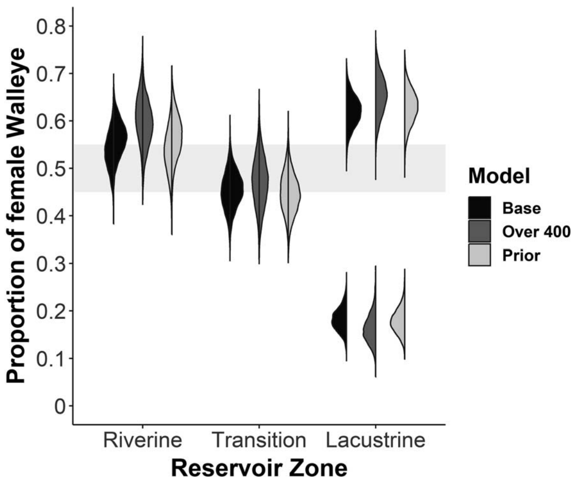

Figure 3. Sensitivity analysis showing half-violin plots of the estimated posterior distributions derived from generalized linear mixed-effects models of mean proportions of female Walleye *Sander vitreus* among three reservoir zones (riverine, transition, and lacustrine) during spring (left half) and fall (right half) in Lake McConaughy, Nebraska, that used data collected in spring and fall 2015 and 2016. The base model represents the initial model and included all fish $\geq$200 mm, the prior model was run using broader priors than the base model, and the over-400 model only included fish $\geq$400 mm. The light-gray shaded rectangle indicates the 0.450–0.550 range.

0.450 and 0.550 were >10.00%, although there was only a 10.65% probability that the proportion of female Walleye was between 0.450 and 0.550 during the spring in the riverine zone on the basis of the simulated posterior distribution. No major differences were observed in the simulated posterior distribution estimates of the female proportions in the lacustrine zone during either season with the over-400 model. Female Walleye proportions estimated from the prior model posterior distribution were within 0.015 of the estimates from the base model (Figure 3), and we did not observe any differences in the meaningful deviations from the 0.450–0.550 range.

Discussion

The greatest seasonal variability was observed in the proportion of female Walleye sampled in the lacustrine zone of the reservoir, where females constituted <20% of the total catch in the spring on the basis of the posterior predictive simulation. This spring pattern is consistent with known Walleye spawning behavior, as males tend to arrive earlier and in greater abundance to the spawning grounds and remain for a longer time frame than females (Ellis and Giles 1965; Bozek et al. 2011). Sampling during this study was not conducted within 1 km of the dam face in either the spring or fall sampling periods, since targeted nighttime electrofishing along reservoir dams has displayed sexually biased capture of male Walleye (Koupal et al. 1997; Katt et al. 2011) and males tend to have a higher probability of occurring at spawning locations than females (Thompson 2009; Katt et al. 2010).

Female Walleye appeared to represent a greater proportion of the fall catch in the lacustrine zone. A greater proportion of the fall catch in nearshore gill nets was made up of younger, small individuals (Schall et al. 2019, 2021), as large adult Walleye likely moved offshore in search of thermal refuge or pelagic forage (Rawson 1957; Bowlby and Hoyle 2011; Hayden et al. 2014). Females have been observed making offshore movements in greater proportions than males in other systems (Raby et al. 2018), and we estimated an elevated proportion of females in fall lacustrine samples. Large female Walleye may have moved into the lacustrine zone during summer months to find thermal refuge or to forage on schools of pelagic Alewife *Alosa pseudoharengus* (Porath and Peters 1997). Fall sampling during this study occurred before water temperatures declined and when nearshore Alewife catch was low (Schall 2016). No sampling occurred offshore to confirm these sex-specific movements in Lake McConaughy, and additional research could provide insight into seasonal sex-specific movements and habitat use in this and other Great Plains reservoirs.

Our evaluation of sex ratios across the three reservoir zones relied on the assumption that mortality was equal among sexes after gill-net entanglement. Limited research has been conducted on the effect of sex on gill-net mortality rates in other species. Simulated gill-net entanglement of mature, migratory Sockeye Salmon *Oncorhynchus nerka* and Coho Salmon *Oncorhynchus kisutch* resulted in higher female mortality (Teffer et al. 2017, 2019). However, female mortality was twice as high as male mortality with increasing water temperature and increased handling, which was likely the result of elevated stress levels and severe physiological impairment occurring as a result of their migratory, spawning behavior (Crossin et al. 2008; Teffer et al. 2017, 2019). Conversely, sex either did not adversely affect gill-net mortality or males experienced higher mortality for several marine fishes (Williams and Schaap 1992; Sulikowski et al. 2018). Currently, no research is available regarding the relationship between sex and gill-net mortality in Walleye. Although it is unlikely that Walleye would experience the same sex-specific gill-net mortality patterns as salmon, further study of the effect of gill-net entanglement on Walleye sexes would provide insight on any effect of sex-specific physiological response on mortality, particularly during the spawning season.

Sensitivity analysis indicated that there was little influence of excluding fish we considered immature or of our selected prior probability distributions. For the over-400 model, we considered fish >400 mm to be mature, as individuals of this length were likely to be $\geq$3 y old (Schall et al. 2021). Others have used similar sizes to consider Walleye sexual maturity, i.e., unknown-sex individuals $\leq$381 mm were considered immature by Myers et al. (2014). The only estimate from the posterior distribution that was substantially different was the spring riverine proportion of females, which was slightly higher. The means and shapes of the estimated proportions of females from the posterior distribution of the prior model were nearly identical to the base model. Overall, these models demonstrate that sex distribution of Walleye >200 or >400 mm in this large Great Plains reservoir was generally close to one female to one male in the riverine and transitional zones but that ratios in the lacustrine zone were likely skewed toward males in the spring and females in the fall.

The distribution of sex ratios may also have an impact on angler exploitation in Great Plains reservoirs. Higher angling catch and harvest rates for females than for males have been observed across northern Walleye populations, regardless of size (Myers et al. 2014). Myers et al. (2014) suggested that the higher angler catch and harvest may be partially explained by female Walleye being more likely to strike a lure because of their higher consumption rates (Schneider and Crowe 1977; Henderson et al. 2003) and earlier vulnerability to harvest since they grow faster than males (Henderson et al. 2003). Conversely, the greater presence of male Walleye at spawning locations has been associated with higher angler exploitation in Lake Erie (Bade et al. 2019). Anglers commonly congregate along the dam during spring at Lake McConaughy and harvest disproportionally more males (K. Pope, personal communication), so perhaps seasonal male-biased harvest in conjunction with increased longevity of male Walleye (Schall et al. 2021) may counteract increased female harvest vulnerability and prevent the reservoir from having a male-biased sex ratio. Additional analysis of Walleye mortality in Lake McConaughy has been suggested to improve estimates (Schall et al. 2021), and sex-specific considerations may be warranted for identifying spatial or seasonal patterns in exploitation.

Developing an understanding of spatiotemporal patterns in Walleye sex ratios can have important implications for interpreting standardized sampling results. Standard sampling recommendations for Walleye include fall gill netting (Bonar et al. 2009), but limited guidance has been provided on the distribution of sampling locations across reservoir spatial scales. Previous research on Lake McConaughy found that sampling efficiency for Walleye remained consistent regardless of random or stratified sampling designs, and size structure was generally consistent among reservoir zones in the fall (Schall et al. 2019). The results of this study demonstrate that sex ratios should have a limited impact on fall sampling, except in the lacustrine zone. If randomized sampling results in a skewed number of lacustrine samples, managers may consider documenting sex of sampled Walleye to avoid issues with age estimation from age–length keys that could alter management interpretation of sampling results.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Data S1. Walleye *Stizostedion vitreum* sampling data, where each row represents a unique fish and includes total length (length; mm); sex assigned after visual observation of the gonads; and the season, year, and reservoir zone in which each individual was sampled. Corresponding R code used in data analysis can be found in the following GitHub Repository: https://github.com/bjschall/McConaughy_Walleye_Sex_Ratios.git

Available: https://doi.org/10.3996/JFWM-22-043.S1 (32 KB XLSX)

Reference S1. Chizinski CJ, Martin DR, Pope KL. 2014. Angler behavior in response to management actions on Nebraska reservoirs. Lincoln, Nebraska: Nebraska Cooperative Fish and Wildlife Research Unit and Nebraska Game and Parks Commission. Federal Aid in Sportfish Restoration Performance Report Project F-182-R.

Available: https://doi.org/10.3996/JFWM-22-043.S2 (1.562 MB PDF)

Reference S2. Colby PJ, McNicol RE, Ryder RA. 1979. Synopsis of biological data on the Walleye *Stizostedion v. vitreum* (Mitchill 1818). FAO Fisheries Synopsis 119.

Available: https://doi.org/10.3996/JFWM-22-043.S3 (4.094 MB PDF)

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