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Does a Bioenergetics Model Accurately Predict Fish Consumption by American White Pelicans? A Case Study on Walleyes in the Tamarac River, Minnesota

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Abstract

The effect of piscivorous birds on fisheries is a growing concern for fisheries managers, especially when native birds consume large quantities of fish. The Red Lakes, Minnesota, fishery is one such example, where congregations of American white pelicans (AWPEs) *Pelecanus erythrorhynchos* forage on spawning Walleyes *Sander vitreus*. We quantified AWPE consumption of Walleyes on the Tamarac River, a major tributary of the Red Lakes, by using empirical diet data collected from lethally sampled birds and separately by using a bioenergetics model. Furthermore, we evaluated the diet and foraging patterns of AWPEs on the river. Camera trap data revealed that AWPEs were foraging nearly completely nocturnally, likely in response to Walleye spawning migrations, with Walleyes accounting for 98% of AWPE diets. The empirical estimate of daily fish consumption from lethally sampled birds was not significantly different from the bioenergetics estimate. Monte Carlo simulations were used to provide estimates of uncertainty in annual Walleye consumption. Based on the simulations, all estimates of annual Walleye consumption between 2014 and 2016 represented < 1% of adult (age ≥ 3) Walleyes in the system and < 2.5% of adult Walleye natural mortality. This amount of Walleye consumption by AWPEs, at current population levels, does not pose a management concern.

The interactions of piscivorous birds and fish stocks have been studied since the early 20th century but have become a topic of increasing interest in the previous two decades, due in part to the expansion of bird populations. Two of the most studied piscivorous bird species in North America are the American white pelican (AWPE) *Pelecanus erythrorhynchos* and the double-crested cormorant *Phalacrocorax auritus*. American white pelicans are large, highly visible birds and are increasing in range and abundance, doubling their population between 1979 and 2001 (King and Anderson 2005). Increasing populations coincide with aquaculture expansion (King and Grewe 2001; King 2005) and the ban of DDT. Several studies suggest that this increase in the AWPE population, in part, may be a response to previous declines caused by DDT prior to the ban (Anderson et al. 1969; Blus et al. 1974; Boellstorff et al. 1985; Donaldson and Braune 1999). However, it is unclear whether the AWPE

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population is still increasing toward pre-DDT levels or whether favorable conditions have allowed them to surpass pre-DDT population levels. High visibility and increased angler awareness of AWPE fish consumption often lead to anglers voicing concern regarding the impact of AWPEs on fisheries. Such is the case on the Red Lakes, Minnesota, which host a large, popular fishery for Walleyes *Sander vitreus*.

The Red Lakes Walleye fishery collapsed in the 1990s as a result of overfishing but has since recovered after a harvest moratorium and an intensive short-term stocking program (Red Lakes Fisheries Technical Committee, 2006 harvest plan for Red Lakes Walleye stocks to the Minnesota Department of Natural Resources [MNDNR]). The Walleye population has been maintained entirely by natural reproduction since 2006; at the time of this study, the population had reached record-high levels of abundance (Kennedy 2013), with standing stock during each of the 5 years prior to this study estimated to be greater than 4.5 million kg (Brown and Kennedy 2018). Recreational and commercial harvests were reopened in 2006, and the Red Lakes now support a highly productive Walleye fishery. Recreational anglers on state waters of Upper Red Lake harvested 105,000 kg of Walleyes during the 2014 harvest year (Brown and Kennedy 2018). The Red Lakes also provide an economically important commercial fishery for the Red Lake Nation, which harvested 436,000 kg of Walleyes during the 2015 harvest year (Brown and Kennedy 2018).

From 2007 to 2017, mean annual natural mortality of Walleyes in the Red Lakes was 32.5% (age ≥ 3) but was highly variable, ranging from 15.5% (in 2015) to 50.2% (in 2013; Brown and Kennedy 2018). During this same period, Walleye spawning stock biomass (SSB) exceeded the upper limit of the optimal range (6.92–12.36 kg/ha [2.8–5.0 kg/acre]; Red Lakes Fisheries Technical Committee, harvest plan) identified in the Harvest Plan for Red Lakes Walleyes and is thus considered "surplus" (Kennedy 2013; Brown and Kennedy 2018). Spawning occurs naturally in the lakes and in tributaries, but the proportion that comes from each component is unknown. Walleyes undergo spawning migrations in several tributaries each spring and, although the magnitude of each has not been quantified, the Tamarac River is thought to have the largest Walleye spawning migration of any of the Red Lakes tributaries.

Relative abundance of Walleyes during their spring spawning migration in the Tamarac River has been estimated during most years since 2000 via spring electrofishing surveys. As the magnitude of Walleye spawning migrations increased with the recovery of the population, electrofishing crews on the river observed an increasing, and substantial, temporary population of AWPEs. These birds are returning from wintering habitats along the Gulf of Mexico and use the river as a temporary feeding ground while forage is abundant and while they wait for ice to recede from nesting sites and feeding grounds further north. In addition to Walleyes, Northern Pike *Esox lucius* and White Suckers *Catostomus commersonii* also migrate into the Tamarac River to spawn prior to and after Walleyes, respectively, but AWPE abundance is greatest during the Walleye migration.

American white pelicans are opportunistic piscivores that display annual and seasonal variation in prey selection relative to available forage (Findholt and Anderson 1995). They are able to forage successfully in water less than 1.5 m deep during day or night (McMahon and Evans 1992) and are known to prey heavily on migrating fish during spring riverine spawning migrations (Scoppettone et al. 2014; Teuscher et al. 2015). Walleyes migrate into riverine spawning grounds at night, preferring water depths of 0.3–1.5 m for spawning (McMahon et al. 1984). The temporal and spatial overlap between the Walleye spawning migration and AWPE use of the Tamarac River for foraging suggests that Walleyes likely represent a substantial portion of AWPE diets during this time. Although previous studies have described AWPE consumption of various game and nongame species and the effect on fish stocks (Hall 1925; Major et al. 2004; Idaho Department of Fish and Game 2009; Frechette et al. 2012; Scoppettone et al. 2014; Teuscher et al. 2015), none has focused on the Walleye as a prey species. Additionally, the majority of AWPE predation studies have been conducted in the western and southeastern USA, with few occurring in the Midwest.

Diet composition and total fish consumption by piscivorous birds are typically evaluated through observation of foraging birds (Hall 1925; Werner 2004), the recovery of tags (typically T-bar anchor or PIT tags) deposited by birds (Frechette et al. 2012; Scoppettone et al. 2014; Teuscher et al. 2015), or the use of bioenergetics models (Madenjian and Gabrey 1995; Major et al. 2004). Observations of foraging birds can be subjective, labor intensive, difficult to validate, and limited by environmental variables (e.g., daylight and line of sight). The use of tag recoveries provides an effective way to measure the impact of AWPEs on fisheries but is expensive, especially for large-scale evaluations, and is not always feasible. Bioenergetics models are a popular cost-effective method for estimating fish consumption by birds (e.g., Glahn and Brugger 1995; Madenjian and Gabrey 1995; Gremillet et al. 2003; Major et al. 2004), but these models are often generalized for broad application to multiple species and use uncertain parameters, which can lead to inaccuracy or uncertainty. Empirical consumption estimates are useful to evaluate bioenergetics model performance and improve the confidence in consumption estimates obtained using bioenergetics models. However, previous studies that have examined AWPE stomach contents used those data to determine diet composition and did not provide total

consumption estimates (Lingle and Sloan 1980; Findholt and Anderson 1995).

We established AWPE population abundance, diet composition, and fish consumption estimates on the Tamarac River during the Walleye migration to quantify the effect of AWPE predation at the Tamarac River on Walleye mortality in the Red Lakes. Furthermore, our empirical consumption data allowed for evaluation of nonintrusive consumption estimates, including those made using bioenergetics models. The objectives of this study were to (1) quantify AWPE consumption of Walleyes in the Tamarac River during their spawning migration and the effect of this mortality on the Red Lakes Walleye population, (2) compare consumption estimates made using empirical data and a bioenergetics model, and (3) describe the diel foraging pattern of AWPEs on the Tamarac River.

METHODS

Study site.— The Red Lakes comprise two large, oval basins (Upper Red Lake and Lower Red Lake) connected by a narrow channel. The combined total surface area of 116,550 ha makes the Red Lakes the largest body of water contained within Minnesota borders. The Tamarac River is the largest tributary to Upper Red Lake and flows 34.9 km into the northeast corner of the basin. The river has a drainage of 815 km^2, including a portion of a 1,295-km^2 peat bog, the largest in the lower 48 states (Janssens et al. 1992). The drainage consists primarily of wetlands, but approximately 35% of the watershed is forested (MNDNR, unpublished data). Water depths typically measure around 1 m but can reach depths of over 3 m near the mouth. This study primarily focused on a 5.5-km reach starting 5.5 km upstream of the mouth (Figure 1). The riparian zone along the study section comprises rice paddies and peat bog, whereas reaches upstream and downstream are dominated by wooded shorelines and moderate development along wooded shorelines, respectively.

American white pelican abundance estimates.— To assess AWPE abundance on the Tamarac River, aerial surveys were conducted from the mouth to approximately 20 km upriver in a fixed-wing aircraft every 2–4 d depending on weather and pilot availability (2014: $n = 7$; 2015: $n = 5$; 2016: $n = 6$). Surveys could not be conducted during the first 9 d of AWPE presence on the river in 2014 (April 20–29) due to weather conditions that made flying unsafe. During this time, and for the first count of 2015, ground counts were used to supplement aerial surveys. Ground
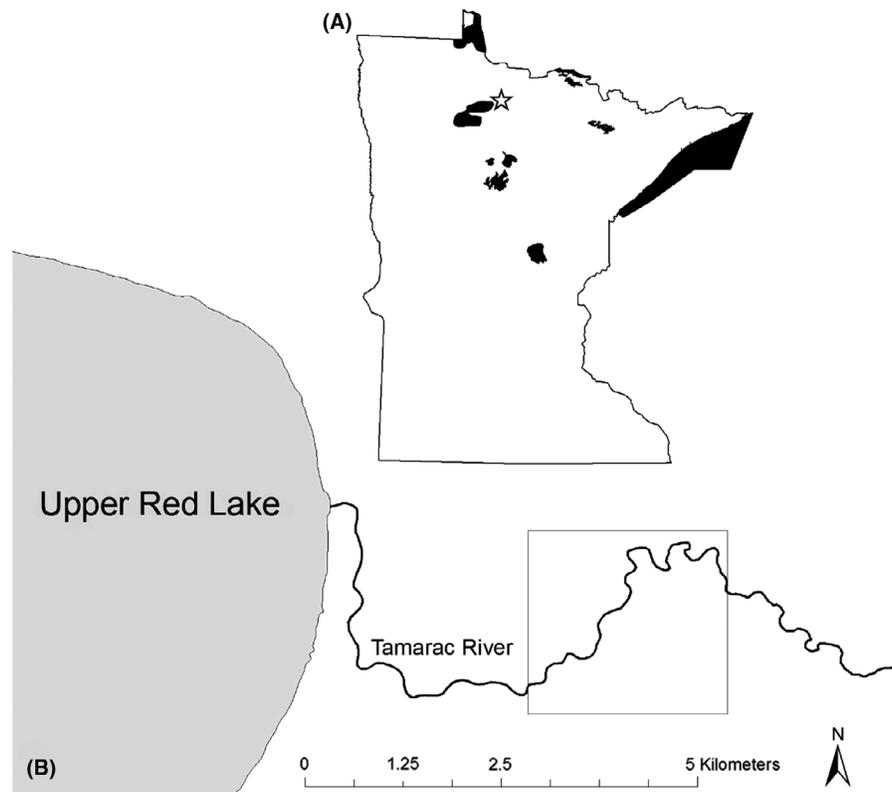

FIGURE 1. (**A**) Base map of Minnesota, with a star marking the location of the Tamarac River; and (**B**) map of the Tamarac River, with a gray box marking the approximately 5.5-km river reach where the highest American white pelican activity occurred.

counts were conducted by observing groups of AWPEs flying from loafing grounds to foraging grounds. Two investigators made independent counts, which were averaged for the final count. Aerial surveys were discontinued when AWPE or Walleye numbers were low and after we concluded that Walleye spawning or AWPE foraging on the river was negligible.

Anecdotal observations by electrofishing crews, which would later be confirmed in this study, suggested that AWPEs foraged primarily after dark, so aerial surveys were conducted early in the morning in an effort to obtain the most accurate estimate of the number of birds foraging on the river the previous night. Aerial surveys consisted of three passes when birds were present and two passes when they were not present, and surveys followed the entire section of river used by AWPEs. A digital camcorder was used to record birds along the length of the river and area immediately surrounding the river mouth (~500-m radius). Video clips from each pass were subsequently viewed on a computer to enumerate AWPE abundance in the study area. The maximum count for a given day was used as the abundance estimate because aerial surveys tend to underestimate abundance due to imperfect detection of present individuals (Pollock and Kendall 1987). American white pelican abundance surveys typically took approximately 8–15 min, dependent on conditions. Flights were conducted between April 19 and May 17, 2014; between April 11 and April 29, 2015; and between April 12 and May 8, 2016.

Daily estimates of AWPE abundance were made assuming that changes in abundance between surveys were linear. Total bird foraging days on the Tamarac River were calculated by summing daily AWPE abundance from when birds were first observed until the day of the last aerial survey. The AWPE abundance in 2015 was much lower than abundances in the two other years, including an aerial abundance estimate of zero during the period that AWPEs were occupying the river. On this occasion, the abundance estimate was made from the maximum number of AWPEs seen on camera traps (see below) at one time.

American white pelican diel foraging patterns.— To assess AWPE foraging patterns on the Tamarac River, camera traps were set throughout the portion of the river where AWPEs were observed (2014: $n = 12$; 2015: $n = 11$; 2016: $n = 10$). Camera traps were placed along a 5-km river segment where MNDNR personnel had observed concentrations of birds foraging in previous years. Both proximity to other camera traps and river morphology were considered when placing each camera trap. Camera traps were placed in locations that covered the longest stretch of river and minimized "blind spots." Photos were taken every 5 min when not triggered by motion and additionally when triggered by motion. If camera traps were

motion triggered, the 5-min interval between photos was reset.

All photos were subsequently examined for AWPEs in the act of foraging. The times when the first AWPE was seen foraging on any camera and the last AWPE was seen foraging on any camera were recorded each night. The time between when the first and last AWPEs were seen foraging was defined as the foraging period. American white pelicans were considered to be foraging when photos displayed actions and/or body positioning similar to that seen during direct observations of foraging AWPEs in the field (e.g., bill dipping, head leaned forward scanning water, multiple birds alertly swimming along shorelines in unison, or large groups appearing to corral fish). Camera traps occasionally captured images of AWPEs foraging outside of the foraging period, and the number of times this occurred was recorded.

Walleye migration and abundance.— Fyke nets were set in the Tamarac River to assess the timing and relative magnitude (i.e., CPUE) of fish spawning migrations while AWPEs were present. Fyke nets (frame = 0.9×1.5 m; bar mesh = 2.5 cm) were set overnight at four standardized locations in 2014 and six standardized locations in 2015 and 2016. Netting events were conducted on April 21–May 9, 2014; April 14–30, 2015; and April 16–May 3, 2016. Half of the net sets were associated with an outside bend and half were associated with an inside bend to capture fish in habitats containing both faster- and slower-moving water. Nets were fished every third day from the day after the river was ice-free until low catches after peak numbers and high water temperatures indicated that the Walleye spawning migration was complete (fyke-netting events: $n = 8$ in 2014; $n = 6$ in 2015; $n = 6$ in 2016). Captured fish were identified to species, sexed, and measured for TL to the nearest millimeter; a subset was weighed to the nearest gram. Biological data collected from a subset of Walleyes were used to establish independent length–weight relationships for males ($n = 234$) and females ($n = 165$). A wet weight–TL relationship was produced using a linear regression of log-transformed lengths and weights, similar to methods described by Anderson and Neumann (1996).

Discharge.— River discharge was measured to quantify water levels in each year, which was used to demonstrate how water level affected AWPE predation. Measurements were made at the downstream end of where AWPE activity occurred. Discharge was measured via the current meter discharge and 0.6-depth method (Turnipseed and Sauer 2010) using 1.0-m river segments.

Diet composition and empirical consumption estimate.— In 2016, AWPEs were sampled via shotgun as close to sunrise as possible to quantify fish consumption and diet composition. Collection events occurred from April 20 to May 1 between 0509 and 0728 hours, with one to

five AWPEs sampled in each shooting event. To avoid educating birds and potentially modifying their behavior and use of the river, specific care was taken to not shoot into large flocks of AWPEs. After collection, food items were obtained by making an incision from the tip of the bill to the sternum and manually removing all contents in the esophagus and stomach. All stomach contents were identified to species after removal. When the level of digestion permitted, fish were sexed and measured for TL. Whenever possible, TLs were applied to sex-specific length–weight equations to estimate fish weight. When fish were too digested to be accurately measured but sex could still be determined, mean length for that sex was entered into the sex-specific length–weight equation. When fish could not be measured or sexed, the mean length of fish from both sexes was entered into a non-sex-specific length–weight equation. The assigned weights for each fish in the stomach were summed to estimate the mass of fish consumed by each bird. It was assumed that all food items recovered from stomachs had been consumed during the current foraging period.

Due to the high metabolism and low gut retention times observed in fish-eating birds, it was highly unlikely that the above assumption was violated. For example, Hilton et al. (2000) examined gut retention times in eight seabird species that were fed two diets and found that gut retention times were typically about 7 h, ranging from 5.8 to 10.8 h. Although Hilton et al. (2000) did not examine AWPEs, it would require AWPEs to have gut retention times approximately 2.5 times longer than the longest retention time from Hilton et al. (2000) to possibly recover food items from the previous foraging period. Considering the level of digestion in recovered fish observed in our study, we are confident that all food items recovered were indeed from the current foraging period and thus that our estimates represented daily consumption.

Bioenergetics model.—Fish consumption estimates for AWPEs were also made using the bioenergetics model for waterbirds from Madenjian and Gabrey (1995). This model uses bird mass to estimate the daily caloric intake required to maintain the bird's mass with an assimilation efficiency of 0.80. Masses of lethally sampled AWPEs ($n = 54$) were obtained after removal of their stomach contents and were used as inputs to the model. An energy density of 6.14 kJ/kg for Walleyes was used from Liao et al. (2004). This estimate is the mean energy density of Walleyes during spring that had TLs larger than 300 mm, which are characteristics exhibited by Walleyes in this study. A White Sucker energy density of 3.69 kJ/kg was used from Bryan et al. (1996). We assumed that percent diet by food item was a good proxy for percent diet by mass because the masses of White Suckers in fyke nets were similar to those of

Walleyes, and all White Suckers recovered from AWPE stomachs were highly digested and could not be measured.

Annual consumption.—We used a Monte Carlo approach that enabled stochasticity and facilitated the propagation of uncertainty in model inputs and parameters to quantify the uncertainty in both empirical and bioenergetics estimates. Monte Carlo simulations consisted of iteratively making random draws from probability density functions fitted to model parameters and inputs and saving the model output (estimated annual Walleye consumption). Variability in Monte Carlo outputs represents the uncertainty in consumption estimates. The Monte Carlo simulation for empirical consumption was conducted by simulating the number of fish consumed; the sex, length, and mass of each consumed fish; and ultimately the total mass consumed for each bird day. The sum of fish consumption from each bird day represents annual Walleye consumption for one iteration of the Monte Carlo simulation. In total, 10,000 simulations each were run for empirical and bioenergetics Monte Carlo experiments.

For the empirical Monte Carlo, probability density functions were fitted to the number of fish eaten per bird (Poisson distribution: $\lambda = 1.96$), fish length for a given sex (normal distribution; male: mean $\pm$ SD = 401 ± 44 mm; female: 511 ± 71 mm), and uncertainty in the log length–log weight regressions (normal distribution; male: mean $\pm$ SD = 0.0 ± 0.085 g; female: mean = 0.0 ± 0.114 g). Prior to simulating length and weight, the sexes of simulated consumed fish were randomly assigned using the sex ratio of consumed fish in lethally collected birds. The bioenergetics model Monte Carlo simulated an AWPE mass for each bird foraging day on the Tamarac River and subsequently inserted the simulated mass into the bioenergetics model. The bioenergetics Monte Carlo simulated bird mass as normal distributions for male (mean $\pm$ SD = 8.6 ± 0.9 kg) and female (5.9 ± 1.5 kg) AWPEs separately because AWPEs exhibit sexual dimorphism in body mass and the distribution of body mass was clearly bimodal. We used culmen length to classify male and female AWPEs following the methods described by Dorr et al. (2005), who reported sex classification accuracies of 95–99%. Sex of AWPEs was assigned randomly based on sex proportions of lethally sampled birds. Literature sources for uncertainty in model parameters (i.e., assimilation efficiency, Walleye energy density, and AWPE metabolic rates) were not available; therefore, the uncertainty in final consumption estimates incurred by uncertainty in model parameters could not be propagated. Thus, the only uncertainty propagated in this simulation was variation in AWPE mass.

Annual AWPE consumption of Walleyes was compared to population and natural mortality estimates for this species from Brown and Kennedy (2018). To evaluate the effect of AWPE predation on the Red Lakes Walleye

population, the percentage of the adult Walleye population that was consumed by AWPEs on the Tamarac River was calculated. The percentage of annual natural mortality that could be attributed to AWPE predation was also calculated for each year of this study. Although this study only quantifies AWPE consumption of Walleyes on the Tamarac River, cursory aerial surveys of AWPE abundance along the perimeter of the Red Lakes and tributaries yielded abundance estimates that were orders of

magnitude lower than those observed on the Tamarac River. Thus, although Walleye consumption estimates presented here are minimum estimates for the entire Red Lakes system, they represent the preponderance of Walleye consumption by AWPEs in the Red Lakes.

Statistics.— Prior to comparing central tendencies from two sample populations, Shapiro–Wilk tests were performed to test for normal distributions. When the distributions were normal, a two-sample *t*-test was performed; if
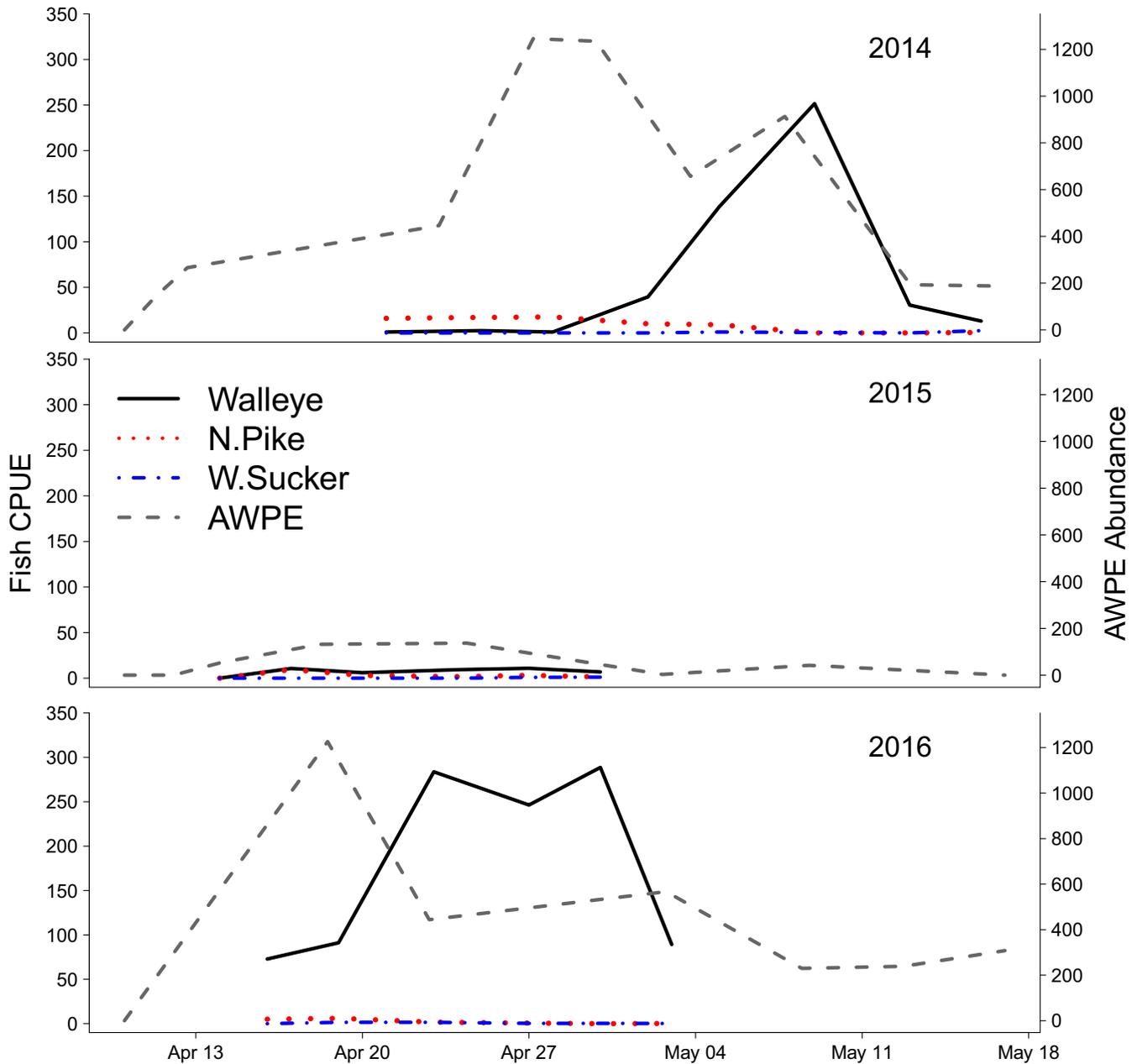

FIGURE 2. Abundances of fish (CPUE; fish/net) and American white pelicans (AWPEs) during the time of the Walleye spring spawning migration and AWPE occupation of the Tamarac River, Minnesota, 2014–2016 (N. Pike = Northern Pike; W. Sucker = White Sucker). [Color figure can be viewed at afsjournals.org.]
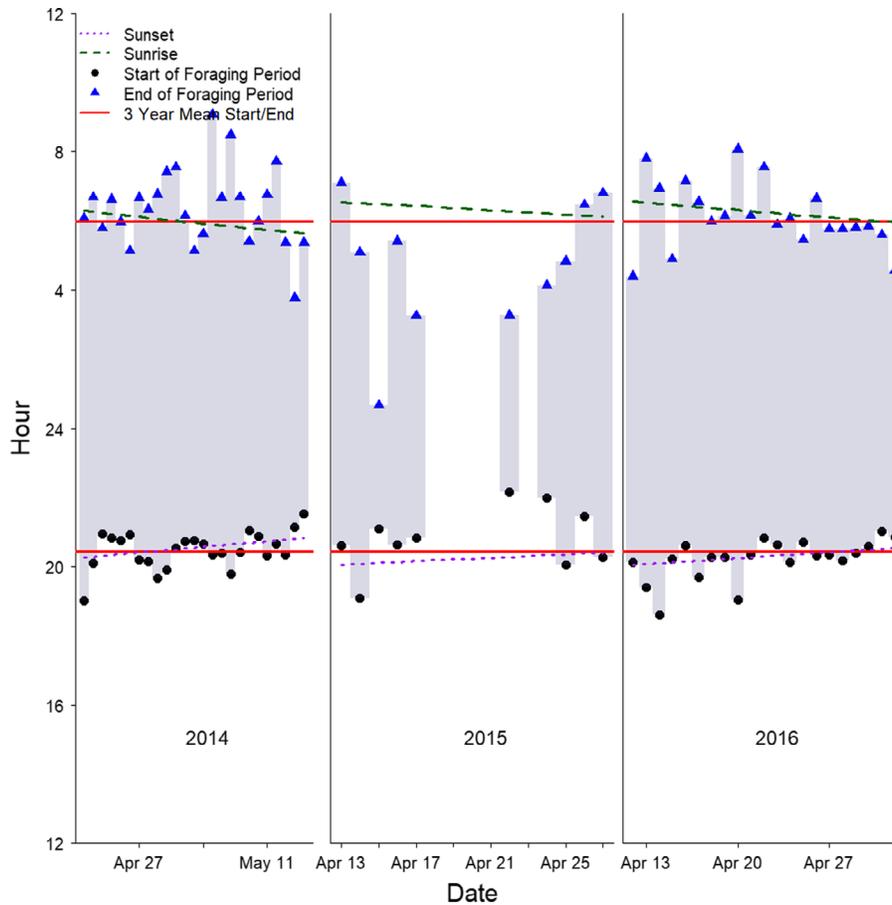
FIGURE 3. American white pelican foraging periods from camera traps on the Tamarac River, Minnesota, during Walleye spawning migrations in 2014–2016. Shaded regions show the time spent foraging each night. Blank dates in 2015 are indicative of nights when there was not a clear start or end to the foraging period (i.e., there was one instance or no instance of pelicans foraging, so a period could not be calculated). [Color figure can be viewed at afsjournals.org.]

either distribution was nonnormally distributed, a Wilcox rank-sum test (Hollander and Wolfe 1999) was performed. Monte Carlo simulations and all statistical tests were conducted using R (Hollander and Wolfe 1999; R Core Team 2017) at an $\alpha = 0.05$ level of significance. Distributions of fish TL were displayed using the kernel density estimation function in R, "density()," which uses a Gaussian kernel to produce smoothed density estimates that integrate to 1.0 (R Core Team 2017).

RESULTS

American White Pelican Abundance Estimates

In 2014, AWPEs were first detected at the Tamarac River on April 20, the first day the river was ice-free (Figure 2). Abundance of AWPEs peaked on May 2 at 1,246 birds. In 2015, AWPEs were first seen on April 13, when ice still covered portions of the river, and abundance peaked on April 18 at 137 birds. In 2016, AWPEs were

first seen on April 13, over a week after the river had been ice-free, and abundance peaked on April 18 at 1,226 birds. American white pelicans arrived prior to the Walleye migration, and AWPE abundance typically peaked prior to the peak of the Walleye migration (Figure 2). Total bird foraging days were much higher in 2014 (16,214) and 2016 (12,994) than in 2015 (1,050).

American White Pelican Foraging Patterns

Camera trap photos indicated that, on average, AWPE foraging began at 2027 hours (95% confidence interval [CI] = 2016–2037 hours) and ended at 0559 hours (95% CI = 0537–0621 hours) across all years (Figure 3), which corresponded to foraging starting ±28 min from sunset and stopping ± 60 min from sunrise. Photos in 2014 and 2016 indicated that AWPEs were feeding throughout this time period, especially in the middle and downstream sections of our study area. In 2015, the frequency of AWPEs in camera trap photos during this time, and in general, was drastically lower. During the 3-year study, 295,840
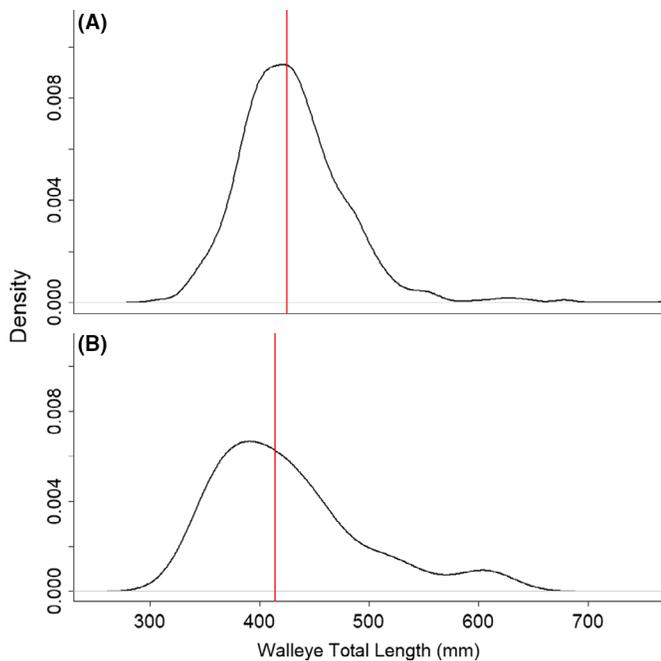
FIGURE 4. Distributions of total length for (**A**) Walleyes captured in fyke nets and (**B**) Walleyes retrieved from American white pelican stomachs. Vertical red lines represent the median values. [Color figure can be viewed at afsjournals.org.]

photos were examined, and AWPEs were seen foraging outside of the aforementioned foraging period a total of 13 times.

Walleye Migration and Abundance

Water levels in 2014 and 2016 were much higher than that in 2015 and resulted in much higher discharges. Mean discharge was 13.88 m^3/s ($n = 8$) in 2014, -0.32 m^3/s ($n = 3$) in 2015, and 10.07 m^3/s ($n = 8$) in 2016. Negative discharge readings were likely attributable to a combination of lake seiche and extremely low flows. Low Walleye CPUE in fyke nets during 2015 compared to 2014 and 2016 suggested that low water levels in 2015 negatively influenced Walleye abundance.

Relative abundance of Walleyes peaked at 251.5, 10.8, and 288.7 Walleyes/net in 2014, 2015, and 2016, respectively (Figure 2). Mean TLs of male Walleyes were 418 mm (2014), 437 mm (2015), and 420 mm (2016); mean female TLs were 467 mm (2014), 509 mm (2015), and 472 mm (2016). Fyke nets were fished from April 21 to May 9, 2014; from April 14 to April 30, 2015; and from April 16 to May 3, 2016.

In all years, the relative abundance of Walleyes was higher than the relative abundances of Northern Pike and White Suckers. Relative abundance peaks for Northern Pike were 17.5 fish/net (2014), 9.3 fish/net (2015), and 6.0 fish/net (2016). White Sucker relative abundances were 2.5, 1.2, and 1.5 fish/net in 2014, 2015, and 2016,

respectively. Northern Pike were typically more abundant near the beginning of the Walleye migration, whereas White Suckers were more abundant toward the end of the Walleye migration.

Diet Composition

Lethal sampling via shotgun in 2016 yielded 54 birds that were collected in the morning between 0509 and 0728 hours. Lethally sampled AWPEs had a mean mass of 8.60 kg (95% CI = 8.35–8.85 kg) for males and 6.16 kg (95% CI = 4.45–7.87 kg) for females. Food items retrieved were 98.1% Walleyes and 1.9% White Suckers. No nonfish food items were observed. Mean TLs of recovered female and male Walleyes were 511 mm (95% CI = 466–557 mm) and 401 mm (95% CI = 387–416 mm), respectively. The mean number of fish in AWPE stomachs was 2.0 fish/bird (95% CI = 1.7–2.3 fish/bird; range = 0–5 fish/bird). The median length of Walleyes retrieved from lethally sampled AWPEs (415 mm) was shorter than the median length of Walleyes collected in fyke nets (425 mm; Figure 4), but the two values were not significantly different ($W = 42,721$, $P = 0.14$). There was not sufficient evidence to suggest that the percentage of females among Walleyes collected from lethally sampled AWPEs (26.8%) was higher than the percentage of females among Walleyes collected in fyke nets (18.6%; $\chi^2 = 2.429$, df = 1, $P = 0.12$).

Consumption Estimates

Empirical fish consumption by lethally sampled AWPEs ranged from 0 to 2,829 g fish·bird^{-1}·d^{-1}. Mean empirical fish consumption by AWPEs was 1,501 g fish·bird^{-1}·d^{-1} (95% CI = 1,309–1,693), and mean Walleye consumption by AWPEs was 1,462 g fish·bird^{-1}·d^{-1} (95% CI = 1,256–1,668). Total fish consumption estimates using the bioenergetics model and mass from the 54 lethally sampled AWPEs ranged from 1,127 to 1,978 g, with a mean of 1,668 g fish·bird^{-1}·d^{-1} (95% CI = 1,621–1,714). Estimates of daily Walleye consumption from the bioenergetics model ranged from 1,104 to 1,938 g fish·bird^{-1}·d^{-1}, and the mean was 1,635 g fish·bird^{-1}·d^{-1} (95% CI = 1,589–1,680). Estimates of fish consumption (g fish·bird^{-1}·d^{-1}) for individual AWPEs were not significantly different between the bioenergetics model and empirical estimates ($W = 1,630$, $P = 0.29$; Figure 5).

Annual Walleye Consumption

In 2014, the mean empirical Walleye consumption estimate from Monte Carlo simulations was 24,068.3 kg (range = 23,503.0–24,731.1 kg) and the mean bioenergetics consumption estimate was 27,075.1 kg (range = 26,990.4–27,159.1 kg; Figure 6; Table 1), which accounted for 2.18% (range = 2.12–2.24%) and 2.45% (range = 2.44–2.45%) of natural mortality, respectively. Mean empirical and
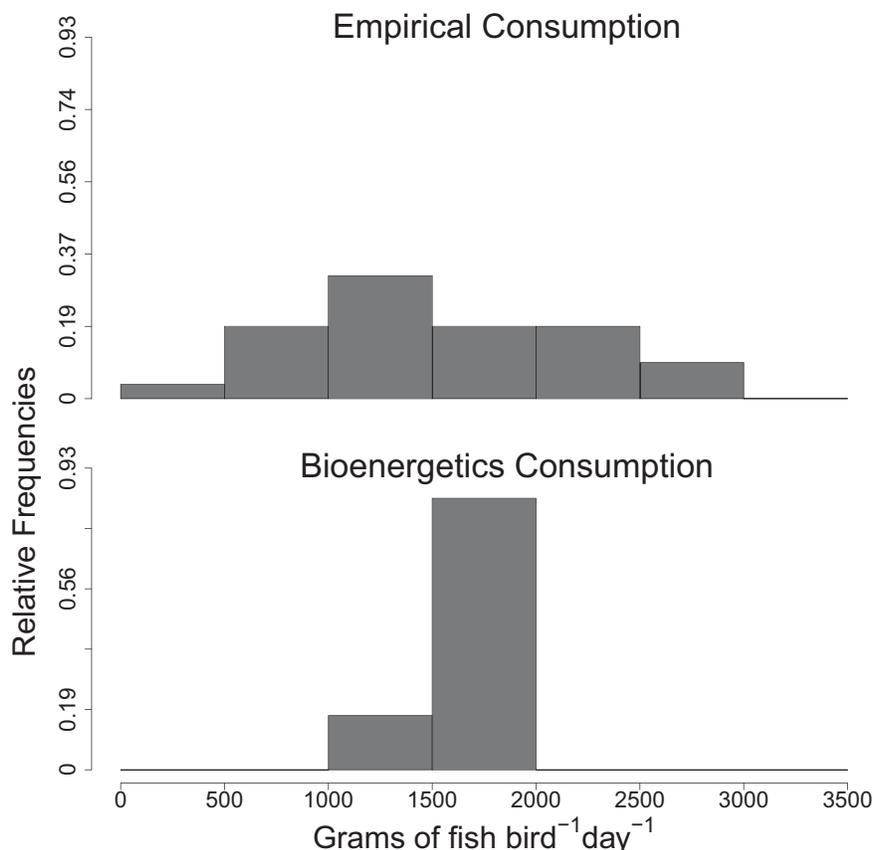
FIGURE 5. Relative frequencies of fish consumption (g fish·bird^{-1}·d^{-1}) based on empirical estimates from American white pelicans that were lethally sampled in 2016 and based on bioenergetics model estimates obtained using weights from lethally sampled birds.

bioenergetics model consumption estimates in 2015 were 1,559.1 kg (range = 1,416.4–1,720.1.0 kg) and 1,753.6 kg (range = 1,729.0–1,777.2 kg), corresponding to 0.18% (range = 0.16–0.20%) and 0.20% (range = 0.20–0.21%) of natural mortality, respectively. The 2016 mean empirical consumption estimate was 19,289.6 kg (range = 18,668.3–19,810.8 kg), accounting for 0.84% (range = 0.82–0.87%) of Walleye natural mortality; the mean bioenergetics consumption estimate was 21,701.0 kg (range = 21,633.1–21,781.4 kg), constituting 0.95% (range = 0.94–0.95%) of natural mortality. Mean consumption from bioenergetics Monte Carlo simulations was on average 11.1% higher than mean consumption from empirical simulations (for all years). Walleye consumption estimates from all Monte Carlo simulations for the 3 years represented less than 1.0% (mean = 0.37%; range = 0.03–0.77%) of the adult (age ≥ 3) Walleyes in the Red Lakes.

DISCUSSION

The effect of avian piscivory on fish stocks is widely variable, ranging from minuscule (<1% of the adult population in this study) to highly impactful (Winfield 1990; Rudstam et al. 2004; Fielder 2008; Teuscher et al. 2015; Cowley et al. 2017). Piscivorous birds can represent substantial portions of fish predation, with estimates as high as 84% annually (Cowley et al. 2017) and 99% seasonally (Winfield et al. 1990), although these estimates likely represent the upper extremes of avian predation on fishes. Therefore, while piscivorous birds clearly have the potential to affect fish stocks, it should not be assumed that all levels of avian predation have negative population-level effects, as demonstrated in this study.

Predicting how piscivorous birds influence fish stocks can be difficult because bird–fish interactions are variable across species (bird and fish) and systems. Specifically, attaining unbiased AWPE diet data poses several challenges. During the first year of this study, we attempted to sample AWPEs by using nonlethal methods. However, our efforts resulted in the collection of biased AWPE diet data due to bird behavior (e.g., regurgitation when disturbed) and fish morphology (spiny dorsal fins) that reduced the effectiveness of forced regurgitation. Lethal sampling enabled greater
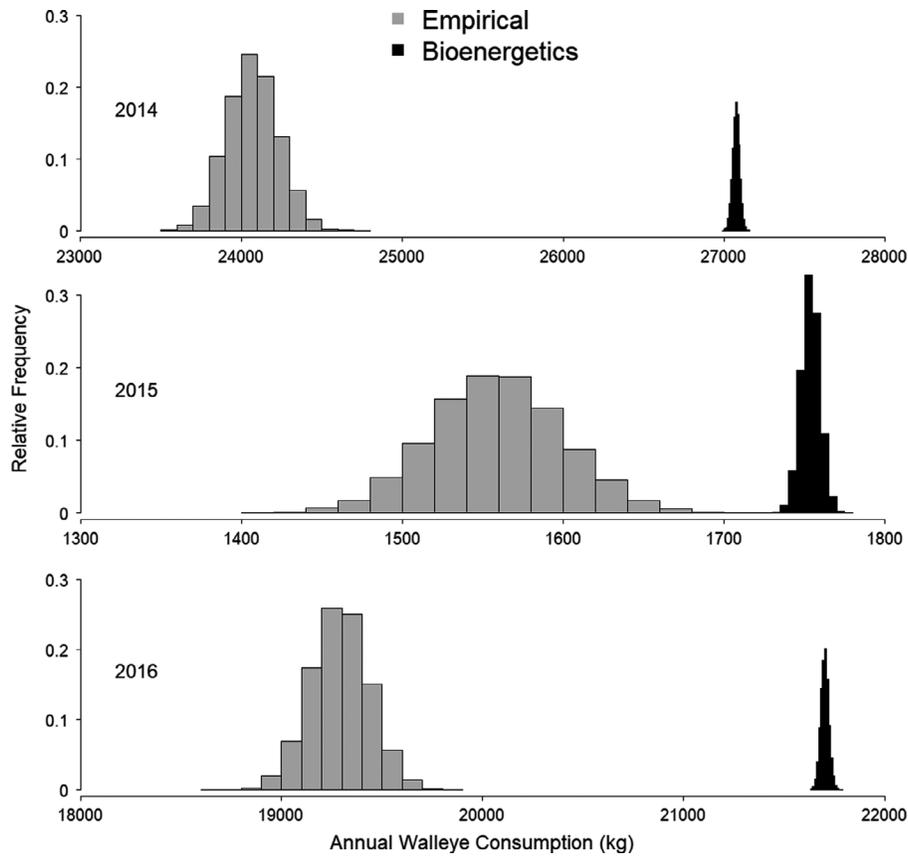
FIGURE 6. Relative frequencies from Monte Carlo simulations of Walleye consumption by American white pelicans, showing variability in estimates when using the empirical method and the bioenergetics model of consumption in each year of the study. Note that the *x*-axis scale differs among years.

TABLE 1. Estimates (number of fish) of American white pelican (AWPE)-induced mortality, natural mortality excluding pelican consumption, harvest mortality, and survival of adult Walleyes (age ≥ 3) in the Red Lakes, Minnesota, during 2014–2016 and the 3-year mean.

Variable	2014	2015	2016	Mean
Walleye population	4,750,438	7,468,843	7,674,127	6,631,136
Harvest	733,796	774,580	652,350	720,242
Natural mortality	1,453,534	1,159,156	3,049,254	1,887,315
AWPE-induced mortality	32,320	2,094	25,902	20,105
Survival	2,530,788	5,533,013	3,946,621	4,003,474

control of the time, location, and number of AWPEs sampled with high certainty that we were obtaining unbiased diet samples. Diet data recovered in this study suggest that AWPEs were not gape limited in their consumption of Walleyes (Figure 4), given that the largest consumed fish were in the 99th quantile of Walleyes from fyke nets.

Nocturnal foraging by AWPEs is not unique to this study (Anderson 1991; McMahon and Evans 1992; Werner 2004); however, the nearly exclusive crepuscular and night-time foraging we observed appears to be unique in the literature. In response to reduced Walleye abundance, AWPE predation on the Tamarac River was much lower during the low-flow year in this study (i.e., 2015). Scoppettone et al. (2014) also reported lower AWPE predation in a low-flow year, as the target prey species, the Cui-ui *Chasmistes cujus*, did not attempt a spawning migration. Conversely, Teuscher et al. (2015) suggested that AWPE predation on Cutthroat Trout *Oncorhynchus clarkii* was higher in low-flow years because trout were more easily captured by wading AWPEs. The mixed results from these studies demonstrate how low-flow scenarios that improve conditions for AWPE foraging can result in increased or decreased predation rates by AWPEs, depending on the system, the targeted fish species, and the magnitude of reduction in flow.

The exploitation of fishes migrating prior to and during AWPE nesting and incubation is not unique to this study

or prey species (Scoppettone et al. 2014; Teuscher et al. 2015). This pattern appears in other pelican species as well, with Whitfield and Blaber (1979) reporting that great white pelicans *Pelecanus onocrotalus* in South Africa followed and preyed on migrating Striped Mullet *Mugil cephalus* during their preincubation period. This suggests that fishes migrating prior to and throughout the pelican nesting and incubation stage likely represent an important food source for pelicans, due to their abundance and availability during a time when pelican energy requirements are elevated by reproductive needs.

Bioenergetics models are useful tools for estimating food consumption and energy demands in individuals and populations of birds (Wiens and Innis 1974; Wiens and Scott 1975; Furness 1978; Madenjian and Gabrey 1995; Madenjian and O'Connor 1999). Many studies have assessed metabolic rates or daily energy expenditure (DEE) of birds to build bioenergetics models. However, the accuracy in these assessments varies greatly (Furness 1978; Birt-Friesen et al. 1989), and there are few examples that compare empirical field estimates of daily food consumption by birds to bioenergetics model outputs. Results from our study and a study by Birt-Friesen et al. (1989) suggest that daily consumption estimates from bioenergetics models for waterbirds that incorporate body mass are similar to empirical consumption estimates, with estimates for a typical bird in our study only differing by 10% (1,668 g [bioenergetics] and 1,501 g [empirical]). Given the challenges associated with producing empirical fish consumption estimates and the agreement between our empirical and bioenergetics estimates, we recommend that investigators use bioenergetics models similar to the approach employed by Madenjian and Gabrey (1995) to estimate the effects of AWPE consumption on fish populations.

Estimated daily fish consumption by AWPEs for our empirical method (1,501 g fish·bird^{-1}·d^{-1}) and the bioenergetics model (1,668 g fish·bird^{-1}·d^{-1}) were comparable to —and intermediate to—estimates from previous studies (Hall 1925; Major et al. 2004; Werner 2004). The field-based estimate of 1,980 g fish·bird^{-1}·d^{-1} from Hall (1925) was higher than either of our estimates, while both of our estimates were higher than the bioenergetics model-based estimate (1,339 g fish·bird^{-1}·d^{-1}) provided by Major et al. (2004). Some of the difference between these estimates may be due to variation in energy densities of prey species or because the AWPEs studied by Hall (1925) and Major et al. (2004) were from different subpopulations than the AWPEs in our study. Both of our estimates were higher than the empirically estimated 1,000 g fish·bird^{-1}·d^{-1} reported by Werner (2004). This discrepancy is likely explained by the inability of AWPEs in the Werner (2004) study to fly long distances or search for food, which presumably lowered their energy requirements.

The inability to incorporate the uncertainties of parameters used in the bioenergetics model (e.g., AWPE assimilation efficiency, Walleye energy density, and AWPE DEE) into Monte Carlo simulations resulted in an underestimate of variability/uncertainty in annual consumption estimates using this method. Conversely, we were able to incorporate major sources of variation (number of fish eaten per bird per day; and the sex, length, and weight of fish) in empirical estimates; thus, variability in empirical Monte Carlo estimates provided a better representation of the uncertainty in consumption estimates. Therefore, our empirical estimates yielded the most reliable approximation of fish consumption and its uncertainty.

For all Monte Carlo simulations in all years, the estimated number of Walleyes consumed by AWPEs on the Tamarac River accounted for less than 2.5% of adult Walleye natural mortality and less than 1.0% of the adult Walleye population. Therefore, this study provides evidence to suggest that despite the presence of a highly visible AWPE population feeding on extremely vulnerable Walleyes during a spawning migration, AWPE predation on Walleyes is not having population-level effects in the Red Lakes. Our results demonstrated that substantial populations of piscivorous birds do not always have a meaningful negative effect on fish stocks, highlighting the need to evaluate the effect of avian predation on fishes on a case-by-case basis. The level of Walleye predation by AWPEs in this study constituted a small portion of the adult population (<1%), leading us to suggest that AWPE predation at the Red Lakes does not warrant management action or concern. High variability in Walleye natural mortality and low AWPE-induced Walleye mortality indicate that factors other than AWPE predation currently regulate the Walleye population in the Red Lakes. However, this study took place when the Walleye population was high and when there was a surplus of SSB. If either of these decline or if AWPE predation increases, managers should consider re-evaluating the effect of AWPEs on the Walleye population of the Red Lakes.

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