FEASIBILITY OF WALLEYE POPULATION SUPPRESSION IN BUFFALO BILL RESERVOIR, WYOMING

by

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ABSTRACT

Buffalo Bill Reservoir, Wyoming is managed as a wild Rainbow Trout *Oncorhynchus mykiss* and Cutthroat Trout *Oncorhynchus clarkii* fishery. Nonnative Walleyes *Sander vitreus* were discovered in 2008, and spring sampling of Walleye indicate natural recruitment and a rapidly expanding population. Walleyes pose a predation threat to the wild trout populations in Buffalo Bill Reservoir. The Wyoming Game and Fish Department (WGFD) is interested in suppressing the Walleye population using mechanical removal with electrofishing and gillnetting during the Walleye spawning period. The purpose of this study was to evaluate the population demographics of Walleyes in Buffalo Bill Reservoir. Age-structured population models were used to estimate the Walleye population growth rate for scenarios with and without Walleye removal. To inform the population models, age-specific fecundity, probability of maturity, natural mortality, and fishing mortality were estimated. Mean asymptotic population growth rate for the five scenarios were estimated as 1.22 (95% CI of 1.05 to 1.37) for no suppression, 1.18 (95% CI of 1.04 to 1.32) for electrofish exploitation, 1.04 (95% CI of 0.88 to 1.19) for gill-net exploitation, 0.91 (95% CI of 0.61 to 1.36) for angler exploitation, and 0.81 (95% CI of 0.66 to 0.96) for angler and gill-net exploitation combined. Results from the age-structured population models suggest that long-term population suppression is a viable goal, and additional gill-net effort and angler harvest incentives should be pursued. During this study the density of mature Walleyes was low, indicating that the population had not yet reached carrying capacity. Analysis of population inertia indicates that the projected abundance of the initial population vector results in a lower population size compared to projected abundance of a population with stable-age distribution. Results from this study will be used to inform cost-effective management decisions regarding the future of the recreational fishery in Buffalo Bill Reservoir. The cost per mature female removed in 2017 was $490.91 and $80.08 for electrofish and gill net removal, respectively. Future suppression efforts should be monitored using population indices of age diversity for female Walleyes.

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Introduction

Historically, many nonnative fish introductions were the result of stocking sport fish (Rahel 2000) and were implemented by natural resource agencies and conservation organizations to improve catch rates, increase angling opportunity, or both, for commercial and recreational fisheries (Rahel and Smith 2018). Sport fish stocking by agencies was often a result of public pressure (Halverson 2008) and the public has an affinity for top-level predators. Thus, top-level predators were the common nonnative sport fishes stocked because they obtain large sizes, provide a sporting catch, and exhibit piscivorous feeding behavior (McMahon and Bennett 1996; Crossman and Cudmore 1999). However, stocking top-level predators has had deleterious effects on recipient fish assemblages (e.g., Rieman et al. 1991; Schoen et al. 2012) and has contributed to the homogenization of freshwater fish assemblages in the USA (Rahel 2000, 2002). However, the stocking of nonnative species to increase their range expansion is now rare and natural resource agencies are currently facing nonnative species expansion through illegal introductions or immigration of nonnative species from a source population (Rahel and Smith 2018). The range expansion by illegal introductions or immigration from source populations of Walleye *Sander vitreus* continues to plague natural resource agencies, particularly in the western United States (McMahon and Bennett 1996; Rahel and Smith 2018).

Walleyes were commonly stocked outside of their native range because of their desirability as a sport fish (McMahon and Bennett 1996; Billington et al. 2011; Fuller 2018), but have had adverse effects on native fish assemblages (Rieman et al. 1991; McMahon and Bennett 1996; Baldwin et al. 2003). In addition to the effects on native fish assemblages, Walleye can also negatively affect trout fisheries in reservoirs. For example, Walleye consumed the majority of stocked Rainbow Trout *Oncorhynchus mykiss* in Seminoe Reservoir, Wyoming (Marwitz and Hubert 1997). Consequently, the stocking strategy shifted to stocking large Rainbow Trout to decrease predation rate (Marwitz and Hubert 1997). Many western US reservoirs have limited natural recruitment of trout and require supplementation of hatchery trout to maintain trout fisheries. In reservoirs with sympatric populations of Walleye and trout, stocking catchable size trout produces a higher return to creel (Wiley et al. 1993; Yule et al. 2000). However, raising catchable size trout is costly and decreases hatchery rearing capacities because of facility constraints (Wiley et al. 1993). In reservoirs where natural trout recruitment occurs, population suppression of Walleye may be a cost-effective alternative to hatchery supplementation.

Population suppression is a popular practice for management of nonnative fish in large waterbodies (e.g., Larson et al. 2003; Martinez et al. 2009; Syslo et al. 2011; Zelasko et al. 2016). Eradication of nonnative species is typically an unrealistic objective; however, suppression is realistic, but effort must be maintained in perpetuity to maintain target abundances (Pine et al. 2007; Propst 2014). Given the high financial cost associated with population suppression, all potential suppression strategies should be evaluated (Govindarajulu et al. 2005; Baxter et al. 2008) prior to implementing a suppression program. One way to predict suppression outcomes is through demographic perturbation analysis. This method can also be effective in estimating the costs of varying suppression strategies (Syslo et al. 2013), which allows agencies to determine the likelihood of having a successful suppression program.

Suppression of Walleye through mechanical harvest (e.g., gill nets) is probable because case histories exist where Walleye have been overexploited in recreational fisheries. For example, high angler effort and low production caused growth overfishing of Walleye populations in lakes close to urban areas in Alberta, Canada (Sullivan 2003). Similarly, a combination of recreation and tribal fisheries caused the collapse of the Walleye fishery in Upper Red Lake, Minnesota, USA indicated by decreasing the spawning stock age structure (Gangl and Pereira 2003). However, increases in exploitation of Walleye populations can result in compensatory increases in individual growth rates and decreases in age at maturity (Spangler et al. 1977). The extent of compensatory responses varies along a latitudinal gradient caused by differences in thermal energy inputs (Lester et al. 2014). For example, exploitation of 17–20% resulted in decreased standing crop (kg/ha) of adult Walleyes in Savanne Lake, Ontario (Baccante and Colby 1996), whereas exploitation of 35% increased standing crop of adult Walleyes by 23% in Big Crooked Lake, Wisconsin (Schmalz et al. 2011). The increase in standing crop in Big Crooked Lake, Wisconsin was caused by increased growth rates and decreased age at maturity (Schmalz et al. 2011).

Understanding the population-level response of a nonnative species to suppression is critical before implementing a suppression program. The amount of suppression effort a natural resource agency can expend is often limited by monetary and logistic constraints, and those constraints dictate the nonnative species response to suppression and the subsequent effects on the target species and ecosystem. Suppression programs can fail to achieve program targets because the nonnative response to the level of suppression effort afforded was not predicted prior to initiating the suppression program. Thus, understanding the demography of the nonnative species and simulating suppression scenarios prior to initiating a suppression program can provide guidance to natural resource agencies on the feasibility of suppression given monetary and logistic constraints. This study was initiated because of the popularity of a wild trout fishery in Buffalo Bill Reservoir, Wyoming and the predicted negative effects of nonnative Walleye on the wild-trout fishery (Johnson 2017). There are currently two management options to maintain the popular wild-trout fishery, replace wild trout consumed by Walleye through stocking or suppress Walleye using mechanical methods. Here, I provide the population demographic data for Walleye in Buffalo Bill Reservoir, Wyoming and use a simulation approach to perform demographic-perturbation with varying harvest scenarios. These results provide the foundation for making informed decisions about implementing a Walleye suppression program in Buffalo Bill Reservoir, Wyoming.

Study Area

Buffalo Bill Reservoir, located at the confluence of the North and South Fork Shoshone rivers, Wyoming, is a water storage reservoir with dam operations administered by the US Bureau of Reclamation. Reservoir elevation at full operating pool is 1,644 m above sea level, maximum surface area is 3,365 ha, and maximum depth is 61 m. From 1994 to 2016, reservoir pool elevation fluctuated by an average of 10.9 m annually (SD = 3.5). From April 15 to June 30 during 1994–2016 reservoir pool elevation increased by an average of 6.7 m (SD = 2.6). Buffalo Bill Reservoir is dimictic, stratifying from June to September (Johnson 2017). The geology of the surrounding watershed consists of erodible volcanic material, and is prone to mass wasting events (Nelson et al. 1980; Kruse et al. 2000). The reservoir experiences low water clarity (mean Secchi depth 1.9 m, SD 1.1; Johnson 2017).

The native fish assemblage in the North and South Fork Shoshone basin consists of Yellowstone Cutthroat Trout *O. clarkii bouvieri*, White Sucker *Catostomus commersonii*, Longnose Sucker *C. catostomus*, Mountain Sucker *C. platyrhynchus*, Mountain Whitefish *Prosopium williamsoni*, Flathead Chub *Platygobio gracilis*, Lake Chub *Couesius plumbeus*, and Longnose Dace *Rhinichthys cataractae*. Nonnative fish present include Walleyes, Lake Trout *Salvelinus namaycush*, Brown Trout *Salmo trutta*, Brook Trout *S. fontinalis*, Common Carp *Cyprinus carpio*, Yellow Perch *Perca flavescens*, Rainbow Trout, and Rainbow Trout x Cutthroat Trout hybrids. Stocking of *Oncorhynchus* spp. has not occurred since 1995 due to sufficient natural recruitment, and

Buffalo Bill Reservoir is the only large reservoir managed by WGFD as a wild *Oncorhynchus* spp. fishery (WGFD 2011).

Walleyes were first detected in Buffalo Bill Reservoir in 2008. Otolith microchemistry analysis of large individuals captured in 2009 and 2010 indicated that they originated outside of waterbodies connected to Buffalo and were illegally introduced to Buffalo Bill Reservoir in 2002 and 2003 (Carleton 2013). Walleyes are not native to Wyoming, but have become established throughout the state. Deaver and Wardell reservoirs, 62 and 71 km respectively from Buffalo Bill Reservoir, are the closest waterbodies containing Walleyes and have the most similar chemical signature of the early life stages of the founder fish captured in Buffalo Bill Reservoir.

Methods

Field Sampling

In 2016, electrofishing was used to capture and mark fish for abundance and angler-exploitation estimates, and in 2017 to obtain catch statistics for an electrofishing suppression scenario. Walleyes were sampled in 2016 from 11 April through 11 May, and in 2017 from 17 April through 4 May using boat-mounted electrofishing at night. The sample timeframe corresponded with Walleyes spawning in Buffalo Bill Reservoir. The primary sample location was a 2-km reach of the northeast shoreline, and was sampled on multiple occasions throughout the sample period. The location was previously identified as spawning habitat (J. Burckhardt, Wyoming Game and Fish Department, personal communication). Approximately 95% of the entire reservoir shoreline was electrofished to identify additional spawning locations; reaches that were unsuitable for electrofishing were excluded from sampling. However, no additional spawning locations were identified. Electrofishing was conducted using two boats with one driver and two netters each. The electrofishing sample periods ended when all captured females were spent, as indicated by lean appearance, collapsed abdomens, and lack of gamete discharge under moderate abdominal pressure (Eschmeyer 1950).

Walleyes were sampled using gill nets in 2016 to recapture fish for an abundance estimate, and in 2017 to obtain catch statistics for the gill-net suppression scenario. Walleyes were sampled in 2016 from 24 May through 8 June, and in 2017 from 17 April through 10 May using sinking monofilament gill nets. Gill nets used in 2016 were 67.1-m long by 1.8-m deep and had 11, 6.1-m long panels with mesh sizes of 1.9-, 3.8-, 5.7-, 3.2-, 4.5-, 6.4-, 2.5-, 5.1-, 7.0-, 7.6-, and 8.3-cm bar measure. Gill nets used in 2017 were 91.4-m long by 1.8-m deep and had three, 30.5-m long panels with mesh sizes of 5.1-, 6.4-, and 7.6-cm bar measure. The gill nets used in 2016 included a wide range of mesh sizes to obtain a representative sample of the Walleye population and the gill nets used in 2017 were composed of larger mesh sizes to target mature female Walleyes and reduce bycatch mortality in suppression efforts. Gill nets were set throughout the reservoir at depths less than 18.3 m in 2016 to obtain a representative sample of the Walleye population for the recapture period of an abundance estimate. Based upon 2016 catches, gill-net sets were strategically concentrated in 2017 to maximize catch rates to obtain catch statistics for a gill-net suppression scenario. Gill nets were set during the evening and fished overnight.

All Walleyes sampled were measured to the nearest millimeter (TL). Weight (g) was recorded for most sampled Walleyes, although inclement weather conditions prevented weight from being collected on some occasions. T-bar anchor tags were used to mark Walleyes for abundance and exploitation estimates. Tags were inserted below the dorsal fin and anchored by the pterygiophore bones (Pine et al. 2012). All Walleyes were fin clipped to estimate tag loss (Pine et al. 2012). The most distal portion of the left pelvic fin of female Walleyes and the anal fin of male Walleyes were clipped to identify sex of fish with shed tags. All captured Walleyes were examined for tags and fin clips.

Sagittal otoliths were collected from euthanized Walleyes (n=907). Otoliths were mounted in clear epoxy, and transversely sectioned about the nucleus using a low speed IsoMet saw (Quist et al. 2012). Thin cross sections (0.8–1.0 mm) were glued to microscope slides and polished using fine grit sand paper until the otolith nucleus and annuli were clearly visible at 40× magnification.

All euthanized Walleyes captured during 2016–2017 were necropsied (Duffy et al. 2000) to determine sex and maturity. Maturity was assessed as a binary response variable of either mature or immature with mature Walleyes identified by fully developed gonads and immature Walleyes identified by underdeveloped gonads. Sex was determined externally for all mature Walleyes released for the tagging study, and immature Walleyes were classified as unknown.

Data Analysis

A length–frequency histogram was constructed from the 2016 gill-net sample to visualize population length structure. The 2016 electrofish and 2017 gill-net and electrofish data were excluded from the length–frequency histogram to avoid biasing population length structure.

Abundance was estimated seperately by gender to account for differences in catchability of male and female Walleyes (Priegel 1970). Abundance of mature Walleyes was estimated using Chapman’s modification of the Lincoln–Peterson estimator (Seber 1982; Williams et al. 2002):

$$\widehat{N} = \frac{(n_1+1)(n_2+1)}{m_2+1} - 1,$$

with estimated variance,

$$\sigma^2 = \frac{(n_1+1)(n_2+1)n_1-m_2)(n_2-m_2)}{(m_2+1)^2(m_2+2)},$$

where n_1 is the number of Walleyes tagged and released in the first capture period, n_2 is the number of Walleyes caught in the second capture period, m_2 is the number of Walleyes caught during both periods, and $\widehat{N}$ is estimated abundance of Walleyes. The first capture period was conducted using night electrofishing during the spawning period. The second capture period was conducted using overnight gillnetting, and began two weeks after the conclusion of the spawning period to allow for adequate mixing. Tag loss was considered negligible for the abundance estimate because all recaptured Walleyes retained their tags. The abundance estimate assumed a closed population with equal catchability of marked and unmarked Walleyes.

Somatic growth of Walleyes sampled in 2016 and 2017 was described using the von Bertalanffy (VBF) growth model. Length-at-age-data (n=907) were used to model growth for both sexes:

$$\mathrm{TL} = L_\infty\left(1 - e^{-K\bullet(Age-t_0)}\right),$$

where L_∞ is maximum theoretical length, K is the growth coefficient, and t_0 is the theoretical length at age 0. Model parameters were estimated using nonlinear least squares regression with the FSA package in R (Ogle 2016; Ogle 2018; R Core Development Team 2018). Differences in growth between male and female Walleyes were assessed by constructing a set of nested VBF models including all possible combinations of sex-specific and sexes-pooled parameters. Model comparison was performed using AIC_c scores, and the model with the lowest score was selected as the top model.

Age-length keys were used to assign ages to unaged fish. Age-length keys were constructed using the FSA package in R (Ogle 2016; Ogle 2018; R Core Development Team 2018). Separate age-length keys were estimated for male and female Walleyes due to differences in somatic growth rates, and separate age-length keys were estimated for 2016 and 2017 samples to account for variability in year-class strength.

Biomass harvested (kg), yield (kg/ha), and standing crop (kg/ha) of mature females were estimated for 2017 using observed and predicted weights. For all Walleyes greater than 150 mm, a $\log_{10}$length-$\log_{10}$weight linear regression was used to predict weights of Walleyes that were not weighed (Neumann et al. 2012). Biomass harvested was estimated by summing the observed and predicted weights of all mature female Walleyes removed in 2017. Yield was estimated as biomass harvested divided by reservoir surface area at full pool. Standing crop of mature female Walleyes was estimated by multiplying the abundance of mature females by mean weight of mature females, and dividing the product by reservoir surface area at full pool.

Probabilities of maturity at length and age (pm_t) were determined using logistic regression with length and age data from Walleyes sampled in 2016 and 2017:

$$pm_t = e^{\beta_0 + \beta_1 \cdot x_t}/(1 + e^{\beta_0 + \beta_1 \cdot x_t}),$$

where β_0 is an intercept coefficient, β_1 is a slope coefficient, and x_t is length or age. Separate maturity models were constructed for male and female Walleyes, because maturation schedules vary by sex (Wolfert 1969; Kocovsky and Carline 2001; Henderson et al. 2003). Lengths at 10%, 50%, and 90% mature (L_{10}, L_{50}, L_{90}) and age at 50% mature (A_{50}) were predicted from logistic models (Chen and Paloheimo 1994; Dux et al. 2011). Predicted probability of maturity at age (pm_t) for female Walleyes was used to estimate fertility rates for matrix population modeling (see below).

Fecundity was estimated gravimetrically, using female Walleyes sampled during spring 2017 (Murua et al. 2003). Ovaries were removed and preserved in a 7% buffered formalin solution. Both ovaries were blotted dry and weighed to the nearest 0.01 g. Subsamples of approximately 1% were removed from the posterior, medial, and anterior sections of both ovaries and weighed to the nearest 0.01 g. Oocytes were enumerated for each subsample, and the number of oocytes in each subsample was divided by subsample weight to calculate relative fecundity (oocytes/g). Mean relative fecundity was estimated by averaging the oocytes/g of all six subsamples. Fecundity was estimated by multiplying relative fecundity by combined ovary weight. Relationships between length, age, and fecundity were assessed using linear regressions. Predicted mean fecundity at age (f_t) from linear models was used to estimate fertility rates for matrix population modeling (see below).

Natural mortality and fishing mortality were estimated and used in population models to assess the feasibility of suppressing the Walleye population. Fishing mortality was assumed to be additive to natural mortality given the low density of Walleyes in the reservoir (Miranda and Bettoli 2007). Instantaneous natural mortality (*M*) was estimated using the meta-analysis function based on maximum age ($t_{\max}$, Hoenig 1983), following recommendations of Then et al. (2015):

$$M = 4.899 \cdot t_{max}{}^{-0.916}.$$

Uncertainty in *M* was estimated using a bootstrapping technique to sample the meta-analysis coefficients 5,000 times with replacement from normal distributions with mean and SE equal to the coefficient estimates and predicted SEs (Then et al. 2015). Instantaneous natural mortality (*M*) was calculated for each simulation and transformed to annual natural survival (*S*): $S = e^{-M}$ (Miranda and Bettoli 2007). Mean *S* was used to estimate age-specific survival of Walleyes age 1 and greater for matrix population modeling of the no suppression scenario (see below).

Annual survival from egg to age 1 (S_0) was estimated from mean fecundity (f), natural survivorship from age 1 to A_{50} ($S^{5.95}$), and the maximum number of recruits per spawner for an average spawner ($\hat{\hat{\alpha}}$), following the recommendations of Purchase et al. (2005):

$$S_0 = \frac{\hat{\hat{\alpha}}}{f \cdot S^{5.95}}.$$

Mean fecundity was estimated from sample data, $S^{5.95}$ was estimated from S and A_{50}, and $\hat{\hat{\alpha}}$ was obtained from the literature (Myers et al. 1999). Uncertainty in S_0 was estimated using a bootstrapping technique to sample $S^{5.95}$ and f 5,000 times with replacement. A beta distribution was used to constrain $S^{5.95}$ to values from zero to one, and a stretched-beta distribution was used to constrain f values to a realistic biological range (Morris and Doak 2002). Minimum and maximum fecundity values from sample data were used to specify the range of stretched-beta distributions. Estimated S_0 was used for matrix population modeling (see below).

Annual angler exploitation (μ_a), was estimated for female Walleyes from tagging data. Angler exploitation was estimated by the proportion of tagged Walleyes that were harvested (Ricker 1975; Pollock 2001). Angler reporting rate was estimated by tagging a subset of fish with high-value ($100) reward tags and assuming 100% reporting rate. A $100 reward has been determined to be high enough to elicit a reporting rate nearing 100% (Meyer et al. 2012). The reporting rate for low-value ($10) reward tags ($\gamma$) was estimated as (Pollock et al. 2001; Meyer and Schill 2014):

$$\gamma = \frac{L_r/L_t}{H_r/H_t},$$

where L_r is the number of low-value tags reported, L_t is the number of low-value reward tags available for capture, H_r is the number of high-value reward tags reported, and H_t is the number of high-value reward tags available for capture. Variance of γ was calculated by (Henny and Burnham 1976; Meyer and Schill 2014):

$$Var(\gamma) = \gamma^2 \left[\frac{1}{L_r} + \left(\frac{\gamma}{L_r}\right)^2 \left(\frac{L_t}{H_t}\right)^2 H_r\right].$$

A subset of Walleyes was double-tagged with low-value reward tags to estimate annual tag loss (Miranda et al. 2002). However, because no double-tagged fish were reported by anglers as single-tagged, the rate of tag loss was assumed to be negligible, and estimated angler exploitation was not adjusted for tag loss.

An adjusted angler exploitation (μ_a) was estimated (Pine et al. 2012):

$$\mu_a = \frac{N_r}{N_0 \gamma},$$

where N_r is the number of tags returned by anglers, N_0 is the number of Walleye tagged, and γ is angler reporting rate. The complement of annual angler exploitation $(1 - \mu_a)$ was used to adjust S of immature and mature female Walleyes ages 6 or greater in the population model for the angler suppression scenario (see below). Uncertainty in μ_a was estimated using a bootstrapping technique to sample γ 5,000 times with replacement and estimate μ_a for each sampled value of γ. A beta distribution was used to constrain γ to values from zero to one. Estimated $\mu_a$was used for matrix population modeling (see below).

Annual electrofish (μ_e) and gill net (μ_g) exploitation was estimated for mature male and female Walleyes:

$$\mu_x = r_x / \widehat{N}_i,$$

where $\widehat{N}_i$ is estimated abundance, r_x is the number sampled by gear x in 2017. Exploitation estimates μ_e and μ_g were used for matrix population modeling (see below).

Age-structured Leslie matrix models were used to estimate Walleye population growth rates (λ) for suppression scenarios including no suppression, electrofish, gill net, angler, and gill net plus angler exploitation, similar to Syslo et al. (2011), Ng et al. (2016), and Fredenberg (2017). An age-structured model was used because otoliths provide an accurate aging structure and fecundity and probability of maturity vary with age. The population models were female based and used post-breeding census timing

(Caswell 2001). Age-specific vital rates (described above) were used to estimate transition elements of a projection matrix Q_s:

$$Q_s = \begin{bmatrix} 0 & 0 & \cdots & F_6 & \cdots & F_{17} & F_{18} \\ S_0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \ddots & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_6 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \ddots & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S_{17} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & S_{18} \end{bmatrix},$$

where F_t is the fertility element for age *t*, and S_t is the survival element of age *t*. Fertility of age *t* was calculated by:

$$F_t = f_t * pm_t * S_t * 0.5,$$

where f_t is mean fecundity at age *t*, pm_t is the proportion mature for age t, and S_t is the annual survival rate for age *t*. The product of f_t, pm_t, and S_t was multiplied by 0.5 because the sex ratio was assumed to be 1:1. Annual survival S_t was adjusted according to suppression scenarios to account for changes in survival and fertility elements caused by suppression efforts. For ages fully recruited to suppression gears, annual survival of age *t* was $S_t - \mu_e$ for electrofish, $S_t - \mu_g$ for gill net, $S_t - \mu_a$ for angler, and $S_t - \mu_g - \mu_a$ for the gill net plus angler scenario. Annual survival of age classes partially recruited to suppression gears was adjusted to account for differences in fishing mortality between immature and mature Walleyes (i.e., $S_t - \mu_x * pm_t$).

Asymptotic lambda (λ) was estimated as the dominant eigenvalue of Q_s using the popbio package in R (Caswell 2001). Asymptotic mean lambda was estimated for all suppression scenarios.

A simulation approach was used to account for sampling uncertainty in vital rates used to parameterize matrices. Fertility and survival elements were calculated from randomly generated vital rates for 5,000 iteratively generated Q_s. The popbio package (Stubben and Milligan 2007) was used to generate vital rates for each replicate of Q_s. Vital rate values of S_t and pm_t were sampled from beta distributions, which are restricted to realistic values between 0 and 1. Vital rate values of f_t were sampled from stretched beta distributions, which were restricted to specified fecundity values that represent the minimum and maximum total fecundity estimates observed throughout the geographic distribution of Walleye populations (Carlander 1997). Asymptotic lambda was estimated for each matrix replicate to provide a distribution of values and evaluate the likelihood of successful population suppression given measurements of uncertainty in asymptotic lambda.

Age-specific abundance of mature female Walleyes and elements in the Q_s were used to estimate the initial population vector (n_0). An age-length key was constructed for female Walleyes sampled in 2017 to assign ages to unaged fish and calculate the proportional frequency of each age sampled (pr_t). Age-specific abundance (N_t) was estimated as the product of $\widehat{N}$ and pr_t:

$$\widehat{N}_t = \widehat{N} * pr_t.$$

Abundance of partially mature age classes was adjusted to account for the abundance of immature females:

$$\widehat{N}_{t_{adj}} = \widehat{N}_t / pm_t.$$

Abundance of immature age classes was estimated with a back-projection procedure. First, the age-specific abundances of spawning-age females was back-projected to determine previous abundances:

$$\widehat{N}_t / S_t = \widehat{N}_{t-1}.$$

Next, past age-specific abundance was multiplied by the age-specific fertility element (F_t) to determine the abundance of offspring produced in the previous year ($\widehat{N}_{0_{t-1}}$):

$$\widehat{N}_{t-1} * F_t = \widehat{N}_{0_{t-1}}.$$

Last, past offspring abundances were forward-projected to determine the abundance of immature age classes:

$$\widehat{N}_{0_{t-1}} * S_0 * S_{t-1} = \widehat{N}_t.$$

This process was repeated for all age classes to back-project the abundances of immature fish.

The initial age structure (n_0) of a population affects short-term population growth until a stable age distribution is reached (Koons et al. 2005). Population inertia (SER) was estimated to determine how n_0 influenced projected abundance relative to a population with a stable age distribution (Koons et al. 2007):

$$SER = \frac{v_1^* n_0}{v_1^* r_0},$$

where v_1^* is the complex conjugate transpose of the dominant left eigenvector, n_0 is the initial abundance vector, and r_0 is the reference vector. Population inertia was estimated with n_0 for each suppression scenario using the popdemo package in R (Stott et al. 2012; R Core Development Team 2018). Upper and lower bounds on population inertia values were estimated using the popdemo package in R (Stott et al. 2012; R Core Development Team 2018).

Personnel costs were used to estimate an annual cost for the gill net and electrofish suppression scenarios. The cost per mature female Walleye removed was estimated using scenario labor costs and the number of mature females sampled during April and May 2017. Personnel costs included three person crews paid at an hourly rate of $45. Crews worked 40 hours each week, and worked 3 weeks for the electrofish scenario and 3.5 weeks for the gill net scenario.

Results

Electrofishing and gillnetting were used to sample 1,676 Walleyes in 2016 and 2017 in Buffalo Bill Reservoir, Wyoming. The majority of Walleyes sampled in 2016 and 2017 were mature male fish sampled by electrofishing (Table 1). Walleyes captured in gillnets during 2016 varied in length from 178 mm to 740 mm TL (Figure 1). Mean length (± 95% CI) of Walleyes sampled with electrofishing was 357 (± 5) mm and gillnetting was 519 (± 14) mm.

Abundance estimates (95% CL) were 914 (564–1,830) mature male and 537 (308–994) mature female Walleyes (Table 2). Prior to sampling in 2017, the density of mature females was 0.16 fish/ha, and standing crop was 0.46 kg/ha. Gill net and electrofish harvest of mature females was 797 kg and yield was 0.24 kg/ha in 2017. Gill net and electrofish harvest removed 52% of estimated total mature female biomass in 2017.

Somatic growth rates differed for male and female Walleyes. The top model had separate L_∞ and K parameters, and the model with all common growth parameters received the highest AIC_C score (Table 3). The model with all separate sexes parameter had strong support with a ΔAIC_C of 1.53 (Table 3), thus von Bertalanffy growth models with separate L_∞ and K and common t_0 were fit for male and female Walleyes (Figure 2).

Female Walleyes in Buffalo Bill Reservoir matured at larger lengths and older ages than males (Figure 3; Figure 4). Mature female Walleyes varied in length from 439 mm to 759 mm, and mature male Walleyes varied in length from 246 mm to 555 mm (Figure 3). Mean lengths at 10%, 50%, and 90% mature were 420 mm, 475 mm, and 513 mm for female and 192 mm, 276 mm, and 358 mm for male Walleyes (Figure 3). Mean age at 50% mature was seven for females and four for males (Figure 4).

Fecundity increased with age (f_t = -158,434(43,146) + 33,845(4,062)·age, r^2 = 0.63, $P < 0.0001$) and length (f_t = -451,773(57,814) + 1,062(94)·length, r^2 = 0.75, $P < 0.0001$). Mean fecundity (± 95% CI) was 195,612 (± 22,372) oocytes/fish and varied from 44,634 (age 6) to 416,924 (age 17; Figure 5; Table 4). Mean relative fecundity was 66,727 oocytes/kg and varied from 48,687 (age 8) to 84,867 (age 17).

Annual survivorship (SD) from egg to age 1 was estimated as 0.00048 (0.00026; Table 5). Annual adult (ages > 1) survival in absence of fishing mortality was estimated as 0.71 (0.032; Table 5). Annual adult survival of ages fully recruited to suppression gears was estimated as 0.21 (0.15) for gill net, 0.63 (0.042) for electrofish, 0.30 for angler

(0.26), and 0.0092 (0.031) for the combined gill net and angler suppression scenarios (Table 5).

Mean asymptotic lambda (95% CI) was 1.22 (1.05–1.37) in absence of fishing mortality (Figure 6). Mean asymptotic lambda varied by suppression scenario and was 1.04 (0.88–1.19) for gill net, 1.18 (1.04–1.32) for electrofish, 0.91 (0.61–1.36) for angler, and 0.81 (0.66–0.96) for the combined gill net and angler scenario (Figure 6). Distribution of asymptotic lambdas differed for the angler scenario relative to the other scenarios due to high standard deviations for age-specific estimates of exploitation (Figure 6; Table 5). Over 99% of simulated lambdas were < 1 for the combined gill net and angler scenario, while less than 1% of simulated lambdas were < 1 for the electrofish and no suppression scenarios (Figure 6).

The inertia of all suppression scenarios was < 1 (Table 6), indicating that projected abundance of n_0 results in a lower density relative to the projected abundance of an initial population vector that exhibits a stable age distribution. The lower bound on inertia for the no suppression and combined gill net and angler scenarios are 0.096 and 0.132, respectively. The upper bound on inertia for the no suppression and combined gill net and angler scenarios are 21,870.390 and 917.986, respectively.

Personnel costs were calculated for electrofish and gill-net suppression scenarios. Personnel costs were estimated at $16,200 for the electrofish and $18,900 for the gill-net suppression effort in 2017. Electrofish effort removed 33 mature female Walleye and gill-net effort removed 236 mature female Walleye. The cost per mature female Walleye removed in 2017 was $490.91 for the electrofish and $80.08 for the gill-net suppression effort.

Discussion

Overfishing is defined as catching more fish than the population can replace through natural reproduction. More specifically, recruitment overfishing is defined as the fishing effort to reduce the spawning stock to a level where recruitment is limiting the population growth (Allen and Hightower 2010). Recruitment overfishing has been implicated in the collapse of several popular commercial (e.g., Atlantic cod *Gadus morhua*) and sportfish (e.g., crappie *Pomoxis* spp.) fisheries (Maceina et al. 1998; Rose 2004). Given that recruitment overfishing has collapsed fish populations, overfishing has been used to reduce population growth rates of nonnative species (Syslo et al. 2011). Similar to other studies that used population-demographic models to evaluate the feasibility of suppressing nonnative species (Syslo et al. 2011; Syslo et al. 2013; Tsehaye et al. 2013; Fredenberg et al. 2017), I found that Walleye could be overfished in Buffalo Bill Reservoir, Wyoming using the fishing effort exerted during this study. Modeled-suppression scenarios in this study predicted a combination of gillnetting and angling will suppress the Walleye population in Buffalo Bill Reservoir, Wyoming. These results are based on estimates for population vital rates obtained from Walleye in Buffalo Bill Reservoir, with the exception of egg to age 1 survivorship that was obtained from the literature (Myers et al. 1999; Purchase et al. 2005). These results are consistent with research used to manage Walleye populations with sustainable harvest of recreational, commercial, and subsistence Walleye fisheries throughout their native range; that is, Walleye fisheries can be overharvested and many studies are evaluating harvest regulations to prevent overfishing (Beard et al. 2003; Schmalz et al. 2016).

The estimated Walleye density was 0.4 fish/ha in Buffalo Bill Reservoir, which is low compared to other populations. For comparison, densities for 85 Walleye populations across North America varied from 0.1 to 168 mature Walleye/ha, with a median density of 14.8 fish/ha (Baccante and Colby 1996). Low population density is promising for reducing the time to achieve management targets in population suppression efforts and early action in population suppression is a common characteristic of successful nonnative species control projects (Simberloff 2009).

Length and age at maturity are commonly used to assess overfishing and establish harvest regulations (Muth and Wolfert 1986; Gangl and Pereira 2003); therefore, these data can also be used in estimating harvest rates required for species suppression. Maturation schedules vary according to thermal energy input (Venturelli et al. 2010). Length at 50% mature varied widely among 59 Walleye populations throughout North America; for example, the mean for male Walleyes was 348 mm and varied from 262 to 444 mm and the mean for female Walleye was 451 mm and varied from 331 to 562 mm (Bozek et al. 2011). Length at maturity for male and female Walleyes in Buffalo Bill Reservoir was within the variability reported in the literature (Bozek et al. 2011), although L_{50} for male Walleyes was near the minimum L_{50} reported. Age at maturity for male and female Walleyes in Buffalo Bill Reservoir was within the variability reported for Walleye populations throughout North America. For example, male Walleyes matured from ages 2 to 9 and female Walleyes matured from ages 3 to 11 in Ontario (Morgan et al. 2003). Decreases in length and age at maturity have been observed during Lake Trout suppression in Yellowstone Lake, Wyoming (Syslo et al. 2011). Future suppression efforts in Buffalo Bill Reservoir should monitor maturity schedules to determine whether Walleye mature at smaller sizes and younger ages in response to increased harvest.

Relative fecundity provides an indicator of the population reproductive potential, and is a good metric to compare among populations. Relative fecundity varies with density and thermal energy inputs, similar to maturation schedules (Baccante and Colby 1996; Schueller et al. 2005; Bozek et al. 2011). Mean relative fecundity of Walleyes in Buffalo Bill Reservoir was within the relative fecundity values reported throughout the range of Walleye populations, which vary from 20,000 to 80,000 eggs/kg (Bozek et al. 2011). The high relative fecundity of Walleyes in Buffalo Bill Reservoir indicates that mature females are obtaining enough resources to produce a high per-capita reproductive output.

Mortality rate estimates are important for determining harvest quotas to sustainably manage Walleye populations (Beard et al. 2003; Schmalz et al 2016). Similarly, estimates of mortality rates are used to determine the feasibility and performance of suppression programs to reduce the population size of undesirable species (Syslo et al. 2013). Catch curve methods are commonly used to estimate total mortality, however, violations of constant recruitment and mortality assumptions precluded estimation of total mortality. Cohort catch curves are often used to estimate total mortality when these assumptions are violated, and should be used in future iterations of population models to provide total mortality estimates that are independent of the estimates of natural and fishing mortality obtained in the study. Natural mortality of Walleyes in Buffalo Bill Reservoir was estimated using a meta-analysis function based on maximum age, which provides reasonable estimates given bounds of uncertainty (Hoenig 1983; Then et al 2015; Maceina and Sammons 2016). The estimate of annual natural mortality in this study was similar to catch-curve estimates of total mortality for an unexploited Walleye population in Pennsylvania that varied from 32 to 41% (Kocovsky and Carline 2001). Estimates of annual exploitation of mature female Walleyes in Buffalo Bill Reservoir for the suppression scenarios were within the estimates reported by Baccante and Colby (1996) for 46 Walleye populations (3-56%), and less than the level (68%) reported for a Kansas population (Quist et al. 2010). The minimum annual exploitation rate resulting in extinction was 33% for a Walleye population that experiences a minimum length of harvest of 400 mm and 2,000 growing degree day > 5 ºC (Lester et al. 2014). Buffalo Bill Reservoir experiences less than 2,000 growing degree days > 5 ºC (Center for Sustainability and the Global Environment 2019). Mean length at 10% mature for female Walleye is 420 mm. Thus, 400 mm provides an appropriate approximation for minimum length of harvest because suppression efforts focused on the removal of mature Walleyes. The estimated annual exploitation for the combined gill-net and angler suppression scenario in this study exceeded 33%, indicating that successful population suppression is an attainable goal.

The population models in this study were deterministic and assume no temporal variation (year) in vital rates. These models also adopted a conservative approach for estimation of survival of immature age classes by using natural mortality values that were indicative of robust cohort survival, which would underestime the efficiacy of the suppresion methods in our models because realistically some cohorts would naturally have poor survival. Furthermore, juvenile survival rates are likely to be subjected to demographic and environmental stochasticity and by using a deterministic approach here the models are overly conservative on the estiamted suppression efficacy. In a more realistic scenario vital rates would vary from year-to-year from environmental and demographic stochasticity, which would decrease the estimated lambda of the population (Case 2000). However, the duration of this study was not sufficient to measure temporal variation in vital rates. Additionally, the models used here are density independent and finite resources will limit population growth rates as abundance approaches carrying capacity. Incorporation of density dependence would improve the demographic assessment of the Walleye population in Buffalo Bill Reservoir. However, a density-dependence parameter would probably have little influence on model results given the exceedingly low Walleye density in Buffalo Bill Reservoir. Variation in vital rates as a function of environmental stochasticity was not included in the model because the functional responses between environmental variables and vital rates are unknown. Developing the functional relationships and incorporating those data in the model would improve the model accuracy.

The suppression scenarios in this study did not evaluate bycatch mortality caused by suppression effort. However, large mesh gillnets were used in gill-net suppression effort during the Walleye spawning period to maximize Walleye catch rates and avoid unnecessary bycatch of salmonid and catstomid species. Future gill-net suppression efforts should consider the trade-off between Walleye removal and bycatch mortality, and adjust the mesh sizes of gillnets nets accordingly. Electrofishing removal effort does not cause bycatch mortality, however, the electrofishing effort does not obtain suppression objectives.

The initial population age distribution influences transient population dynamics (Koons et al. 2007); therefore, initial population age structure is an important consideration for population suppression. The population inertia analysis suggested that the initial population vector (n_0) resulted in lower projected abundances compared to projected abundances from a population with a stable age distribution, and this was similar for all suppression scenarios. Projected abundances are expected to be lower than anticipated from a stable age distribution because of the higher proportion of immature Walleyes in the population. The modeled n_0 indicated strong year classes of immature Walleyes are present in the population. Thus, increased electrofish and gill-net catches of mature female Walleye are anticipated as the strong year classes mature.

Cost analysis indicates that gillnetting is a more cost-effective suppression method than electrofishing. However, incorporating recreational angling in suppression efforts could also be a cost-effective strategy. Angler incentive programs have been used effectively in other fisheries to control undesirable nonnative fish (Friesen and Ward

1999; Hansen et al. 2010). For example, an angler incentive program to control a nonnative Lake Trout in Lake Pend Oreille, Idaho paid $15 per Lake Trout removed by anglers. Angler catch was 72% of total catch during Lake Trout removals in 2006 (Hansen et al. 2008). However, additional removal methods are an important complement to angling because angler harvest is likely to decrease as the population declines. Angler catch for the Lake Pend Oreille Lake Trout suppression program declined to 22% of total catch by 2014 (Wahl et al. 2016).

A population indicator should be monitored to evaluate future suppression efforts. Populations with multiple cohorts of mature spawners are more resilient to overfishing and environmental variation compared to populations with missing cohorts of mature spawners (Hseih et al. 2010). Age diversity of mature females can be calculated using the Shannon diversity index, and provides an indicator to assess population suppression (Gangl and Pereira 2003). Low diversity index values indicate few mature age classes and low resilience to recruitment failure (Marteinsdottir and Thorarinsson 1998). In addition to the Shannon diversity the maximum length and age of Walleyes captured in suppression efforts should be monitored to provide simplistic indicators of suppression success.

Results from this study indicate that Walleye in Buffalo Bill Reservoir have typical somatic growth, maturation, and fecundity compared to other Walleye populations. Walleye vital rates appear to be limited by low thermal energy input despite low population density. Without suppression efforts the Walleye population is expected to rapidly increase; however, the simulations described here indicate that successful suppression can be obtained using a combination of gill net and angler removal efforts. Continually updating the population model during the suppression efforts and incorporating environmental variation in the vital rates will improve the accuracy of the model outputs. Given the population model used here was data rich, it may be unrealistic to update the data in the model each year. In this case, more simplistic measures can be used to track suppression success such as the Shannon’s diversity index for the age structure of mature females and catch per unit effort of mature females. Defining measurable targets for success in a suppression program is important to gauge the progress of suppression efforts. Once targets are established, continuing to monitor the Walleye population and updating the model used here will provide the information necessary for adapting the Walleye suppression program to conserve the wild trout fishery.

Table 1. Number of immature and mature Walleyes sampled by gear in Buffalo Bill Reservoir, Wyoming during spring 2016 and 2017.

			Mature	
Year	Gear	Immature	Female	Male
2016	Electrofish	216	82	371
	Gill net	96	58	12
2017	Electrofish	45	33	514
	Gill net	4	236	9

Table 2. Abundance estimates ($\widehat{N}$) , standard error (SE), and 95% confidence limits by sex for mature Walleyes in Buffalo Bill Reservoir, Wyoming in 2016.

			95% confidence limit	
Sex	$\widehat{N}$	SE	Lower	Upper
Male	914	263.5	564	1,830
Female	537	147.7	308	994

Table 3. Model selection results of von Bertalanffy growth models with sex effects on parameters for Walleyes sampled from Buffalo Bill Reservoir, Wyoming during spring 2016 and 2017. Models are ranked by AIC$_c$ values from lowest to highest.

Model	*df*	AIC$_c$	Δ AIC$_c$
$TL = L_\infty[sex]\left(1 - e^{-K[sex] \bullet (Age - t_0)}\right)$	6	5918.15	0
$TL = L_\infty[sex]\left(1 - e^{-K[sex] \bullet (Age - t_0[sex])}\right)$	7	5919.34	1.18
$TL = L_\infty[sex]\left(1 - e^{-K \bullet (Age - t_0[sex])}\right)$	6	5921.91	3.77
$TL = L_\infty\left(1 - e^{-K[sex] \bullet (Age - t_0[sex])}\right)$	6	5925.98	7.83
$TL = L_\infty[sex]\left(1 - e^{-K \bullet (Age - t_0)}\right)$	5	5938.50	20.36
$TL = L_\infty\left(1 - e^{-K[sex] \bullet (Age - t_0)}\right)$	5	5943.62	25.47
$TL = L_\infty\left(1 - e^{-K \bullet (Age - t_0[sex])}\right)$	5	5970.58	52.43
$TL = L_\infty\left(1 - e^{-K \bullet (Age - t_0)}\right)$	4	6001.45	83.31

Table 4. Fecundity (*f*; SE) and proportion mature (*pm*; SE) estimated from regression analyses for Leslie matrix population models of suppression scenarios for the Walleye population in Buffalo Bill Reservoir, Wyoming.

Age	*f*	*pm*
6	44,634 (19,522)	0.078 (0.065)
7	78,478 (15,808)	0.530 (0.131)
8	112,323 (12,315)	0.938 (0.042)
9	146,168 (9,297)	1
10	180,012 (7,364)	1
11	213,857 (7,417)	1
12	247,701 (9,423)	1
13	281,546 (12,474)	1
14	315,390 (15,981)	1
15	349,235 (19,703)	1
16	383,079 (23,537)	1
17	416,924 (27,437)	1
18	450,769 (31,379)	1

Table 5. Mean female Walleye annual survival rates (*S*) and standard deviations (SD) for the Walleye population in Buffalo Bill Reservoir, Wyoming by suppression type used in Leslie matrix population model scenarios.

Age	No suppression	Gill net	Electrofish	Angler	Gill net and angler
0	4.8×10^{-4} (2.6×10^{-5})	4.8×10^{-4} (2.6×10^{-5})	4.8×10^{-4} (2.6×10^{-5})	4.8×10^{-4} (2.6×10^{-5})	4.8×10^{-4} (2.6×10^{-5})
1–5	0.71 (0.032)	0.71 (0.032)	0.71 (0.032)	0.71 (0.032)	0.71 (0.032)
6	0.71 (0.032)	0.67 (0.036)	0.70 (0.033)	0.30 (0.26)	0.26 (0.070)
7	0.71 (0.032)	0.43 (0.096)	0.67 (0.036)	0.30 (0.26)	0.065 (0.073)
8	0.71 (0.032)	0.24 (0.15)	0.64 (0.041)	0.30 (0.26)	0.011 (0.035)
9–18	0.71 (0.032)	0.21 (0.15)	0.63 (0.042)	0.30 (0.26)	0.0092 (0.031)

Table 6. Inertia of initial population vector (n_0) with upper and lower bounds for the projection matrix of mean vital rates for a no suppression scenario in Buffalo Bill Reservoir, Wyoming.

Scenario	Inertia, lower bound	Inertia, n_0	Inertia, upper bound
No suppression	0.096	0.666	21870.39
Gill net	0.119	0.535	5884.58
Electrofish	0.100	0.640	19470.91
Angler	0.116	0.446	10988.43
Gill net and angler	0.132	0.397	917.99

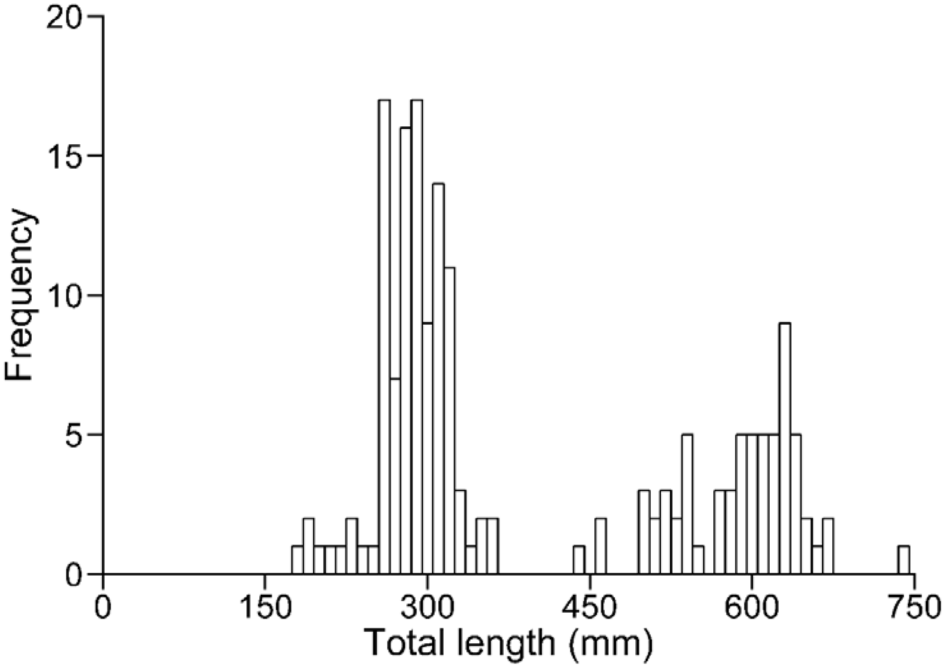

Figure 1. Length-frequency distribution of Walleyes sampled with gill nets in Buffalo Bill Reservoir, Wyoming during April and May 2016.

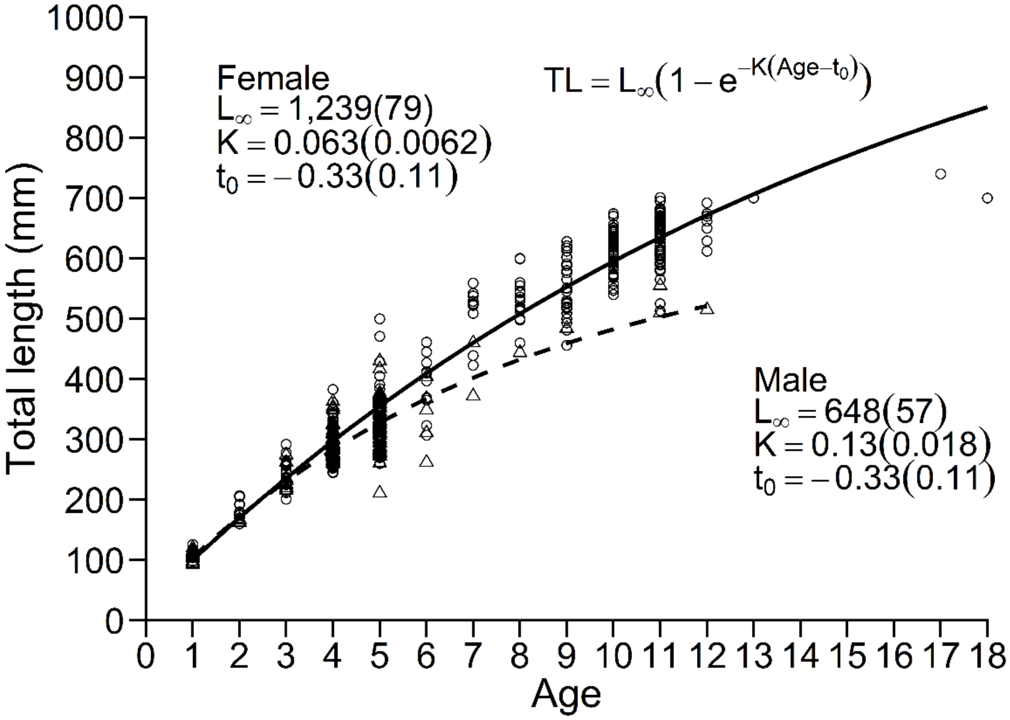

Figure 2. Length-at-age and von Bertalanffy growth models for female (circles, top) and male (triangles, bottom) Walleyes sampled from Buffalo Bill Reservoir, Wyoming, during spring 2016 and 2017.

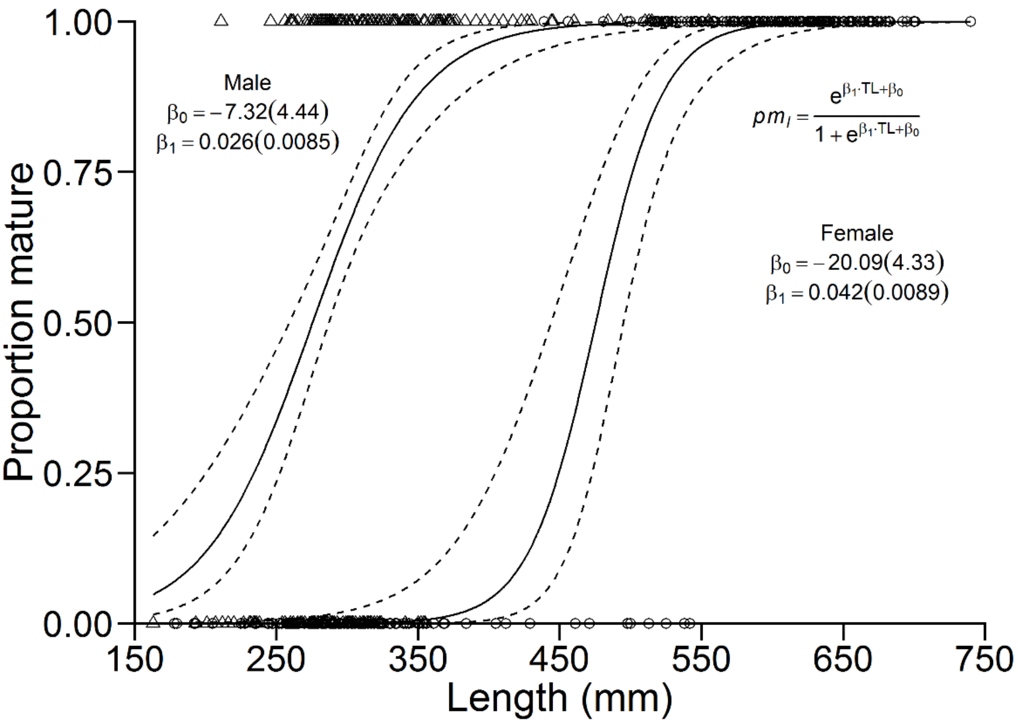

Figure 3. Logistic-regression models for length at maturation of female (circles, right) and male (triangles, left) Walleyes sampled from Buffalo Bill Reservoir, Wyoming during Spring 2016 and 2017, including 95% confidence intervals (dashed lines).

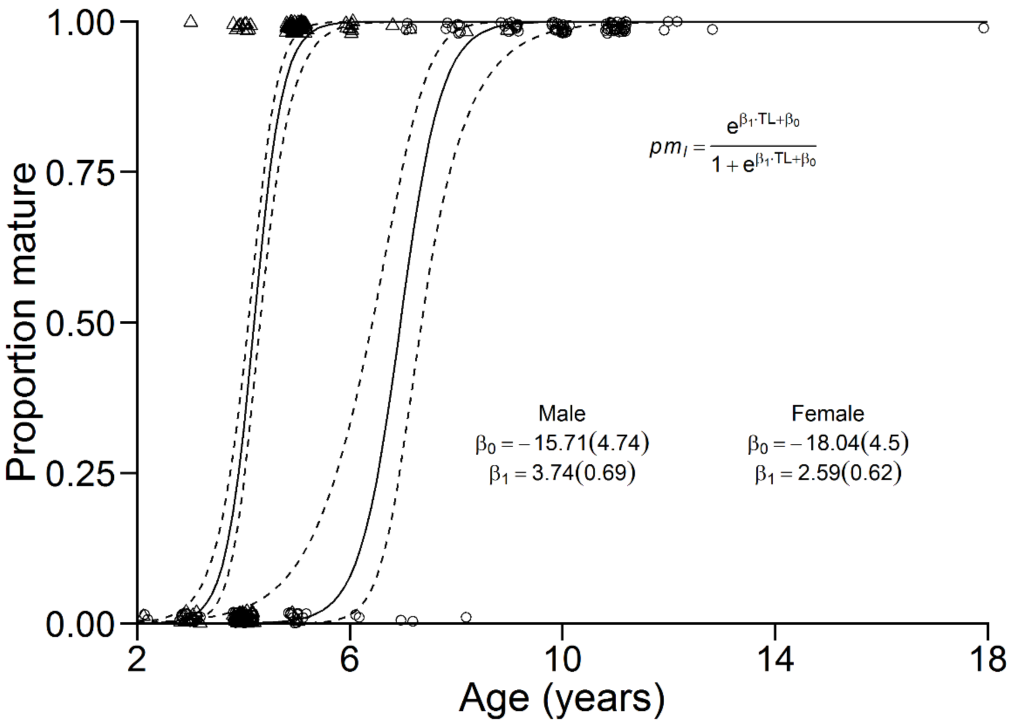

Figure 4. Logistic-regression models for age at maturation of female (circles, right) and male (triangles, left) Walleyes sampled from Buffalo Bill Reservoir, Wyoming during spring 2016 and 2017, including 95% confidence intervals (dashed lines).

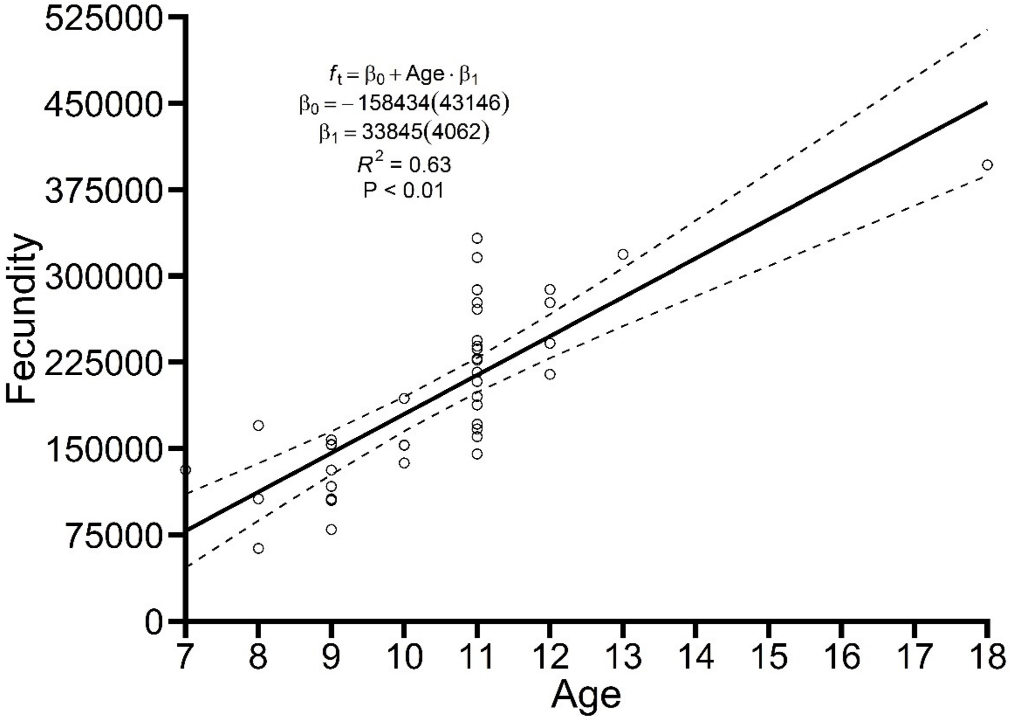

Figure 5. Linear regression model for fecundity at age of female Walleyes sampled from Buffalo Bill Reservoir, Wyoming during spring 2017, including 95% confidence intervals (dashed lines).

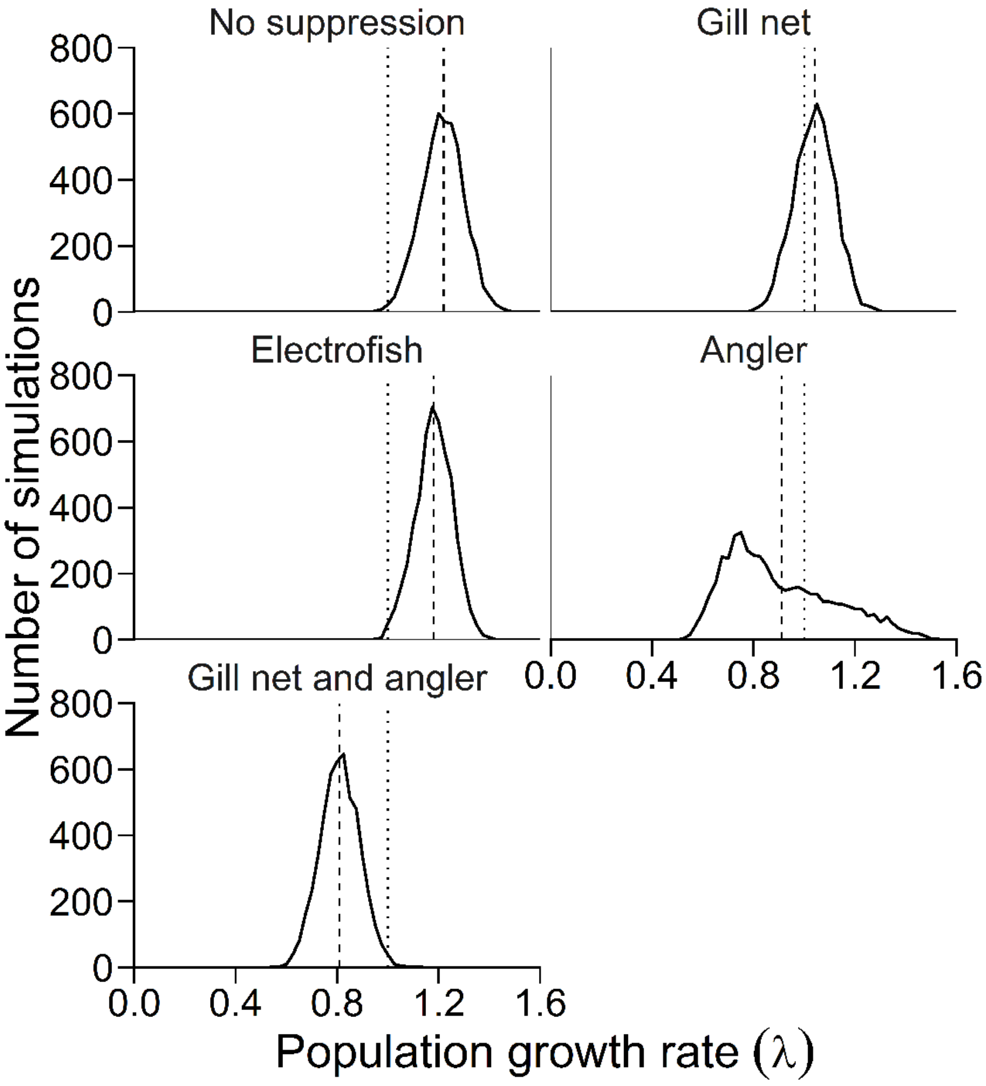

Figure 6. Distribution of asymptotic population growth rate from simulations of no suppression, gill net, electrofish, angler, and combined gill net and angler scenarios for Walleye in Buffalo Bill Reservoir, Wyoming. Heavy dashed lines indicate mean lambdas for each scenario and light dashed lines indicate a stable population (λ=1).

APPENDIX A

SENSITIVITY AND ELASTICITY ANALYSIS

Sensitivity is the influence of an absolute change in a transition element on asymptotic λ, and elasticity is the influence of a proportional change in a transition element on asymptotic λ (Caswell 2001). Sensitivity and elasticity analyses were conducted using Q_s for the no suppression scenario. Sensitivity analysis was performed following the methods of Caswell (1978):

$$s_{ij} = \frac{v_i * w_j}{<w,v>},$$

where v_i is the ith element of the left eigenvector of matrix Q_s, w_j is the jth element of the right eigenvector of matrix Q_s, and $< w, v >$ is the scalar product of the left and right eigenvectors of matrix Q_s. Elasticity (e_{ij}) was estimated (Caswell 1978):

$$e_{ij} = \frac{a_{ij}}{\lambda} * s_{ij},$$

where a_{ij} is the i, j transition element of matrix Q_s. Sensitivity and elasticity analysis were performed using the popbio package in R (Stubben and Milligan 2007). Confidence limits (95%) on sensitivity and elasticity values were calculated as the 2.5th and 97.5th percentiles of the sensitivity and elasticity of each transition element for the 5,000 matrix replicates of Q_s (see above).

Sensitivity analysis indicated that asymptotic lambda was most sensitive to changes in egg to age 1 survivorship for all suppression scenarios (Table 9). Sensitivity values for survival elements of ages one to five were equal, and sensitivity values for mature age classes decreased with increasing age for all suppression scenarios (Table A.1). Elasticity analysis indicated that the relative influence of matrix elements on asymptotic lambda decreased with increasing age for mature age classes (Table A.2).

Elasticity values were equal for survival elements of ages zero to five, and indicated that survival rates of immature fish have the greatest relative influence on asymptotic lambda. Elasticity values of suppression scenarios indicated that increasing fishing mortality of immature age classes would provide the greatest decrease in asymptotic lambda.

Table A1. Sensitivity of asymptotic population growth to mean matrix elements of projection matrices for no suppression (NS), gill net (GN), electrofish (EF), angler (AG), and combined gill net and angler (GN + AG) scenarios for a Walleye population in Buffalo Bill Reservoir, Wyoming. Matrix elements are mean annual survival rates (S_t) and fertility values (F_t) at age *t.*

Matrix element	NS	GN	EF	AG	GN + AG
F_6	$2.29 \cdot 10^{-6}$	$7.20 \cdot 10^{-6}$	$2.80 \cdot 10^{-6}$	$1.64 \cdot 10^{-5}$	$3.49 \cdot 10^{-5}$
F_7	$1.31 \cdot 10^{-6}$	$4.56 \cdot 10^{-6}$	$1.64 \cdot 10^{-6}$	$5.44 \cdot 10^{-6}$	$1.11 \cdot 10^{-5}$
F_8	$7.54 \cdot 10^{-7}$	$1.88 \cdot 10^{-6}$	$9.13 \cdot 10^{-7}$	$1.80 \cdot 10^{-6}$	$8.77 \cdot 10^{-7}$
F_9	$4.33 \cdot 10^{-7}$	$4.24 \cdot 10^{-7}$	$4.86 \cdot 10^{-7}$	$5.98 \cdot 10^{-7}$	$1.22 \cdot 10^{-8}$
F_{10}	$2.48 \cdot 10^{-7}$	$8.32 \cdot 10^{-8}$	$2.57 \cdot 10^{-7}$	$1.98 \cdot 10^{-7}$	$1.33 \cdot 10^{-10}$
F_{11}	$1.43 \cdot 10^{-7}$	$1.63 \cdot 10^{-8}$	$1.36 \cdot 10^{-7}$	$6.58 \cdot 10^{-8}$	$1.45 \cdot 10^{-12}$
F_{12}	$8.18 \cdot 10^{-8}$	$3.21 \cdot 10^{-9}$	$7.21 \cdot 10^{-8}$	$2.18 \cdot 10^{-8}$	$1.58 \cdot 10^{-14}$
F_{13}	$4.70 \cdot 10^{-8}$	$6.30 \cdot 10^{-10}$	$3.81 \cdot 10^{-8}$	$7.23 \cdot 10^{-9}$	$1.72 \cdot 10^{-16}$
F_{14}	$2.70 \cdot 10^{-8}$	$1.24 \cdot 10^{-10}$	$2.02 \cdot 10^{-8}$	$2.40 \cdot 10^{-9}$	$1.87 \cdot 10^{-18}$
F_{15}	$1.55 \cdot 10^{-8}$	$2.43 \cdot 10^{-11}$	$1.07 \cdot 10^{-8}$	$7.95 \cdot 10^{-10}$	$2.04 \cdot 10^{-20}$
F_{16}	$8.88 \cdot 10^{-9}$	$4.77 \cdot 10^{-12}$	$5.65 \cdot 10^{-9}$	$2.64 \cdot 10^{-10}$	$2.22 \cdot 10^{-22}$
F_{17}	$5.10 \cdot 10^{-9}$	$9.36 \cdot 10^{-13}$	$2.99 \cdot 10^{-9}$	$8.74 \cdot 10^{-11}$	$2.41 \cdot 10^{-24}$
F_{18}	$2.93 \cdot 10^{-9}$	$1.84 \cdot 10^{-13}$	$1.58 \cdot 10^{-9}$	$2.90 \cdot 10^{-11}$	$2.84 \cdot 10^{-26}$
S_0	251.837	265.255	254.798	225.436	229.852
$S_1 – S_5$	0.168	0.176	0.170	0.150	0.153
S_6	0.163	0.173	0.166	0.281	0.243
S_7	0.136	0.121	0.138	0.168	$4.64 \cdot 10^{-2}$
S_8	$9.63 \cdot 10^{-2}$	$3.95 \cdot 10^{-2}$	$9.43 \cdot 10^{-2}$	$7.29 \cdot 10^{-2}$	$9.03 \cdot 10^{-4}$
S_9	$6.47 \cdot 10^{-2}$	$9.75 \cdot 10^{-3}$	$5.91 \cdot 10^{-2}$	$2.92 \cdot 10^{-2}$	$1.21 \cdot 10^{-5}$
S_{10}	$4.24 \cdot 10^{-2}$	$2.26 \cdot 10^{-3}$	$3.60 \cdot 10^{-2}$	$1.13 \cdot 10^{-2}$	$1.57 \cdot 10^{-7}$
S_{11}	$2.71 \cdot 10^{-2}$	$5.11 \cdot 10^{-4}$	$2.14 \cdot 10^{-2}$	$4.31 \cdot 10^{-3}$	$1.98 \cdot 10^{-9}$
S_{12}	$1.70 \cdot 10^{-2}$	$1.14 \cdot 10^{-4}$	$1.25 \cdot 10^{-2}$	$1.61 \cdot 10^{-3}$	$2.45 \cdot 10^{-11}$
S_{13}	$1.04 \cdot 10^{-2}$	$2.49 \cdot 10^{-5}$	$7.11 \cdot 10^{-3}$	$5.92 \cdot 10^{-4}$	$2.99 \cdot 10^{-13}$

Table A1. Continued.

Matrix element	NS	GN	EF	AG	GN + AG
S_{14}	$6.13 \cdot 10^{-3}$	$5.39 \cdot 10^{-6}$	$3.93 \cdot 10^{-3}$	$2.14 \cdot 10^{-4}$	$3.60 \cdot 10^{-15}$
S_{15}	$3.42 \cdot 10^{-3}$	$1.15 \cdot 10^{-6}$	$2.06 \cdot 10^{-3}$	$7.53 \cdot 10^{-5}$	$4.31 \cdot 10^{-17}$
S_{16}	$1.72 \cdot 10^{-3}$	$2.37 \cdot 10^{-7}$	$9.80 \cdot 10^{-4}$	$2.48 \cdot 10^{-5}$	$5.10 \cdot 10^{-19}$
S_{17}	$6.60 \cdot 10^{-4}$	$4.14 \cdot 10^{-8}$	$3.57 \cdot 10^{-4}$	$6.53 \cdot 10^{-6}$	$5.91 \cdot 10^{-21}$

Table A2. Elasticity of asymptotic population growth to mean matrix elements of projection matrices for no suppression, gill net, electrofish, angler, and combined gill net and angler scenarios for a Walleye population in Buffalo Bill Reservoir, Wyoming. Matrix elements are mean annual survival rates (S_t) and fertility values (F_t) at age t.

Matrix element	NS	GN	EF	AG	GN + AG
F_6	$2.34 \cdot 10^{-3}$	$8.63 \cdot 10^{-3}$	$2.95 \cdot 10^{-3}$	$2.26 \cdot 10^{-2}$	$5.34 \cdot 10^{-2}$
F_7	$1.57 \cdot 10^{-2}$	$6.01 \cdot 10^{-2}$	$1.99 \cdot 10^{-2}$	$3.75 \cdot 10^{-2}$	$7.42 \cdot 10^{-2}$
F_8	$2.28 \cdot 10^{-2}$	$4.09 \cdot 10^{-2}$	$2.69 \cdot 10^{-2}$	$3.16 \cdot 10^{-2}$	$3.64 \cdot 10^{-3}$
F_9	$1.82 \cdot 10^{-2}$	$6.98 \cdot 10^{-3}$	$1.89 \cdot 10^{-2}$	$1.45 \cdot 10^{-2}$	$1.25 \cdot 10^{-5}$
F_{10}	$1.28 \cdot 10^{-2}$	$1.47 \cdot 10^{-3}$	$1.23 \cdot 10^{-2}$	$5.92 \cdot 10^{-3}$	$1.31 \cdot 10^{-7}$
F_{11}	$8.75 \cdot 10^{-3}$	$3.43 \cdot 10^{-4}$	$7.71 \cdot 10^{-3}$	$2.33 \cdot 10^{-3}$	$1.69 \cdot 10^{-9}$
F_{12}	$5.82 \cdot 10^{-3}$	$7.80 \cdot 10^{-5}$	$4.72 \cdot 10^{-3}$	$8.96 \cdot 10^{-4}$	$2.13 \cdot 10^{-11}$
F_{13}	$3.80 \cdot 10^{-3}$	$1.74 \cdot 10^{-5}$	$2.84 \cdot 10^{-3}$	$3.38 \cdot 10^{-4}$	$2.64 \cdot 10^{-13}$
F_{14}	$2.44 \cdot 10^{-3}$	$3.83 \cdot 10^{-6}$	$1.68 \cdot 10^{-3}$	$1.25 \cdot 10^{-4}$	$3.22 \cdot 10^{-15}$
F_{15}	$1.55 \cdot 10^{-3}$	$8.32 \cdot 10^{-7}$	$9.87 \cdot 10^{-4}$	$4.60 \cdot 10^{-5}$	$3.88 \cdot 10^{-17}$
F_{16}	$9.77 \cdot 10^{-4}$	$1.79 \cdot 10^{-7}$	$5.73 \cdot 10^{-4}$	$1.67 \cdot 10^{-5}$	$4.63 \cdot 10^{-19}$
F_{17}	$6.10 \cdot 10^{-4}$	$3.83 \cdot 10^{-8}$	$3.30 \cdot 10^{-4}$	$6.04 \cdot 10^{-6}$	$5.46 \cdot 10^{-21}$
F_{18}	$3.79 \cdot 10^{-4}$	$8.13 \cdot 10^{-9}$	$1.89 \cdot 10^{-4}$	$2.17 \cdot 10^{-6}$	$6.98 \cdot 10^{-23}$
S_0–S_5	$9.61 \cdot 10^{-2}$	0.118	0.100	0.116	0.131
S_6	$9.38 \cdot 10^{-2}$	0.110	$9.70 \cdot 10^{-2}$	$9.33 \cdot 10^{-2}$	$7.78 \cdot 10^{-2}$
S_7	$7.81 \cdot 10^{-2}$	$4.97 \cdot 10^{-2}$	$7.71 \cdot 10^{-2}$	$5.57 \cdot 10^{-2}$	$3.65 \cdot 10^{-3}$
S_8	$5.53 \cdot 10^{-2}$	$8.90 \cdot 10^{-3}$	$5.02 \cdot 10^{-2}$	$2.42 \cdot 10^{-2}$	$1.26 \cdot 10^{-5}$
S_9	$3.71 \cdot 10^{-2}$	$1.91 \cdot 10^{-3}$	$3.13 \cdot 10^{-2}$	$9.68 \cdot 10^{-3}$	$1.32 \cdot 10^{-7}$
S_{10}	$2.43 \cdot 10^{-2}$	$4.43 \cdot 10^{-4}$	$1.90 \cdot 10^{-2}$	$3.76 \cdot 10^{-3}$	$1.71 \cdot 10^{-9}$
S_{11}	$1.56 \cdot 10^{-2}$	$1.00 \cdot 10^{-4}$	$1.13 \cdot 10^{-2}$	$1.43 \cdot 10^{-3}$	$2.16 \cdot 10^{-11}$
S_{12}	$9.75 \cdot 10^{-3}$	$2.23 \cdot 10^{-5}$	$6.60 \cdot 10^{-3}$	$5.34 \cdot 10^{-4}$	$2.67 \cdot 10^{-13}$
S_{13}	$5.96 \cdot 10^{-3}$	$4.89 \cdot 10^{-6}$	$3.76 \cdot 10^{-3}$	$1.96 \cdot 10^{-4}$	$3.26 \cdot 10^{-15}$

Table A2. Continued.

Matrix element	NS	GN	EF	AG	GN + AG
S_{14}	$3.52 \cdot 10^{-3}$	$1.06 \cdot 10^{-6}$	$2.08 \cdot 10^{-3}$	$7.10 \cdot 10^{-5}$	$3.93 \cdot 10^{-17}$
S_{15}	$1.97 \cdot 10^{-3}$	$2.26 \cdot 10^{-7}$	$1.09 \cdot 10^{-3}$	$2.50 \cdot 10^{-5}$	$4.69 \cdot 10^{-19}$
S_{16}	$9.89 \cdot 10^{-4}$	$4.65 \cdot 10^{-8}$	$5.19 \cdot 10^{-4}$	$8.21 \cdot 10^{-6}$	$5.56 \cdot 10^{-21}$
S_{17}	$3.79 \cdot 10^{-4}$	$8.13 \cdot 10^{-9}$	$1.89 \cdot 10^{-4}$	$2.17 \cdot 10^{-6}$	$6.43 \cdot 10^{-23}$

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